GENETICS OF COTTON FIBER ELONGATION

A Dissertation

by

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Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

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August 2013

Major Subject: Plant Breeding

ABSTRACT

Fiber elongation (ability to stretch before breaking) is one of the key components in determining overall yarn quality. Elongation in U.S. upland cotton (*G. hirsutum* L.) has remained largely neglected due to: absence of monetary incentives for growers to produce high elongation cotton; lack of research interests among breeders; and absence of a reliable fiber testing system for elongation. This study was conducted to determine the genetics of cotton fiber elongation via a diallel and generation means analysis (GMA). Findings from this study should lay the foundation for future breeding work in cotton fiber elongation.

Of the seven distinctive upland parents used for the diallel study, general combining ability was far more prominent than specific combing ability for fiber elongation. Cultivar PSC 355 and Dever experimental line were the two parents identified as good combiners for fiber elongation in this study. The slight negative correlation between fiber elongation and strength remained true. Highly significant negative correlation was observed between fiber upper half mean length and elongation. Both Stelometer and HVI elongation measurements correlated well with values of 0.85 and 0.82 in 2010 and 2011, respectively. For the six families used in the GMA analysis, additive genetic control was prevalent over dominance effect. Based on the scaling test, no significant epistatic interaction was detected for fiber elongation. As expected, additive variance constituted a much larger portion of total genetic variation in fiber elongation than the dominance variance. On average, larger numbers of effective factor

were identified in fiber elongation than all other fiber traits tested, suggesting that parents used in the GMA study are carrying different genetic materials/ loci for fiber elongation. Considerable gains in fiber elongation may be achieved by selectively crossing these materials in a pure-line breeding scheme while holding other important fiber traits constant.

ACKNOWLEDGEMENTS

I would like to thank my committee chair, Dr. C.W. Smith, and my committee members, Dr. Eric Hequet, Dr. Steve Hague, Dr. Tom Cothren and Dr. Yog Raj (special appointment member) for their support and guidance throughout the course of this research.

I would like to also thank Cotton Improvement Lab, technician Mrs. D. Deno, fellow graduate students and student workers at the lab for their help in managing my field plots in College Station. Thanks to the Fiber and Biopolymer Research institute, Lubbock for providing the fiber testing instrument and allowing me to perform my fiber analysis. I also want to extent my gratitude to Monsanto Fellowship in breeding, Texas A&M AgriLife Research, and Cotton Inc. for funding my Ph.D. research at Texas A&M University.

Finally, thanks to my parents and friends for their patience and encouragements for the past few years.

NOMENCLATURE

Elo-H	Fiber elongation (HVI)
Elo-S	Fiber elongation (Stelometer)
GCA	General combining ability
GxE	Genotype by environment interaction
HVI	High volume instrument
Mic	Micronaire (HVI)
SCA	Specific combining ability
Str-H	Fiber strength (HVI)
Str-S	Fiber strength (Stelometer)
UHML	Upper-half mean length (HVI)
UI	Uniformity index

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CHAPTER I

INTRODUCTION

Based on the recent National Cotton Council statistics, cotton (*Gossypium spp.)* production covers roughly 13.6 million acres of farmland in the United States (U.S.) with an estimated annual production of 15 million bales. It is currently projected that 12.9 million bales of cotton produced in the U.S. will be exported in 2012, which accounts for more that 80% of total cotton produced in the U.S. (National Cotton Council, 2012). Of all the cotton grown in the U.S., more than 95% of cultivars grown are Upland type cotton (*G. hirsutum* L.) while Pima type (*G. barbadense*) accounts for the remainder of total acreage. Texas is the largest producer of upland cotton with an annual acreage of approximately five million acres (Cotton Incorporated, 2012). Due to the increased exportation demands and quality expectations, it is important for U.S. cotton to remain competitive not only in yield but also in fiber quality.

In recent years, modernization in yarn and textile industries has mandated that U.S. cotton meet certain international quality criteria. For textile manufacturers, better yarn production requires cotton fibers with improved spinning performance. Previous spinning studies have shown that stronger yarns are often spun with fibers that are long, strong and fine (Gregory et al., 2012; Joy et al. 2010). Currently, there are two commonly used spinning systems worldwide. The rotor spinning system is a high speed system that utilizes fibers with shorter staple length (about 25.4 mm) and good tenacity. This type of system was used predominantly in the U.S. in the early 90s, and most of the

cotton produced domestically was specifically targeted for such a system. Ring spinning is a slower spinning technique often used with higher quality fibers (longer staple length and finer fibers) to produce finer and stronger yarns (Foulk, 2007). Recent shifts in consumer preference for a better quality end product have caused many textile manufacturers to adopt ring spinning technology to meet the demands. According to statistics from the International Textile Manufacturers Federation (ITMF, 2012), there were 110 million ring spinning spindle capacity installed in China as of 2009 as demand for rotor spun yarn steadily declined over the years. With such a large capacity for ring spun type yarn, it is inevitable that U.S. growers would want to produce higher quality fibers for better global marketability and that breeders would want to develop better cotton cultivars to meet the demand. Concomitantly, as textile manufacturers constantly strive for higher output, cotton fibers are also subjected to harsher processing environments. The only way to keep up with such high throughput is to have cotton with improved tensile properties (strength and elongation).

For fiber quality measurement, the High Volume Instrument (HVI) (Uster, 2012a) has been the industry standard in the U.S. since the 1980s (Bradow and Davidonis, 2000). HVI measures fiber strength (kN m kg^{-1}), upper half mean length (mm), micronaire (units), color, elongation (%) and uniformity index (ratio) for every cotton bale produced in the United States. Currently, pricing is based on a combination of strength, length, uniformity index, micronaire, color and trash content as determined by HVI, and premiums are given when cotton exceeds certain quality traits to promote production of higher quality cotton (National Cotton Council, 2012). The monetary

incentive has been a huge driving force for breeders to improve certain fiber traits, especially those thought to be associated with yarn quality such as length, strength and uniformity index. However, these fiber data may not always be a good indicator for the actual yarn performance. May and Jividen (1999) showed only moderate correlation between various fiber traits and their corresponding yarn performance. To better improve yarn quality, breeders always should consider the importance of every fiber property prior to making selections. Crop improvement programs usually focus on traits with high heritability that correlate positively with yield (Scholl and Miller, 1976).

Fiber elongation is valuable information that is often neglected by breeders and the industry due to various reasons. HVI is a high speed and low cost method for obtaining repeatable elongation. However, the lack of standardized calibration cotton samples for HVI elongation renders elongation measurements unreliable from machine to machine (Benzina et al., 2007), and there is no incentive to improve fiber elongation in modern cotton cultivars because it is not part of the cotton pricing structure. The effect of fiber elongation on yarn work-to-break has been inconclusive also. Studies by Green and Culp (1990) indicated that fiber elongation is slightly negatively correlated with yarn strength. Benzina et al. (2007) tested fiber bundle elongation with a modified version of a tensile testing instrument (UT 350®) (Tensometric Company Ltd.) and proposed that fiber elongation is crucial in determining the overall work-to-break for fiber bundles, which is a function of strength and elongation. Moreover, Benzina et al. verified that the negative correlation for fiber bundle elongation and fiber strength was

weak and concluded that simultaneous improvement of fiber elongation and strength is feasible.

Fibers with strength in the premium range, but with lower elongation, may actually rupture more easily than fibers that have moderate strength but superior elongation values. Cotton markets currently consider cotton with strength above 294.2 kN m kg^{-1} (30 g/tex) to be strong regardless of elongation, and this can be a false classification of true fiber tensile properties. Instead, to truly measure fiber tensile properties, work-to-break may be a superior measurement than relying on either strength or elongation alone. According to Meredith (1945), if Hooke's Law were to be obeyed, work-to-break is the area under the stress-strain curve up to the maximum force. In the sense of fiber and textile quality, the work-to-break reflects the total amount of energy needed to rupture a bundle of fibers of a specified weight.

Stelometer (Uster, 2012b) is an improved version of the Pressley strength tester. It is used to measure fiber bundle elongation and strength (the Pressley cannot measure elongation). A constant rate of load is applied to break a fiber bundle, and cotton standards for Stelometer are used to calibrate the instrument. It allows for accurate and repeatable strength and elongation measurements. However, although more reliable, Stelometer elongation is often not fully utilized due to the lower testing speed and the limited amount of fiber properties obtainable compared to the current HVI system. A good comparison between HVI and Stelometer measured elongation and strength from multiple representative upland cotton cultivars would definitely be useful in gauging the

pros and cons of each instrument. The need to accurately and precisely measure elongation may be growing with increasing interest in fiber elongation.

Genetic fixation may be defined as maintaining stable inheritance of favorable alleles or traits over generations of selection. Additive genes with high heritability often allow for rapid genetic fixation and gain. In upland cotton, genetic gain in fiber quality traits such as fiber length and strength has been less than desired. Some studies even suggested fiber strength to be negatively correlated with increased fiber yield (Miller and Rawling, 1967; Scholl and Miller, 1976; Tang et al., 1996). Therefore, in order to truly improve spinning performance and not sacrifice yield, it is important for breeders to consider alternative fiber traits such as fiber elongation. A quantitative trait loci (QTL) study on fiber elongation has shown that fiber elongation is a highly heritable trait with minimal genotype by environment (GxE) effect even under stressful environments (Paterson et al., 2003). In addition, genetic studies completed on various upland type cotton cultivars have shown fiber elongation to have predominantly additive gene action, more so than fiber strength in many cases (May and Taylor, 1998; Quisenberry, 1975).

There are various experimental designs a breeder could use to investigate genetic components for traits of interest. Identifying a proper design could lead to optimized genetic gain over the years with minimal resources (Fehr, 1991). High general combining ability (GCA), indicating additive gene action and high narrow sense heritability (h^2), among a given set of parents is desirable. Assuming a relative high h^2 for elongation, as indicated by some studies, it would be interesting to further dissect the genetic component governing elongation in several prominent upland cotton cultivars in

Texas. To do so, a diallel analysis without reciprocals (model 1, method 2) could be used to partition the general combining ability (GCA) and specific combining ability (SCA) for elongation (Griffing, 1956a; Griffing 1956b). In addition, generation means analysis could be used to further investigate gene actions involved in elongation via multiple generations generated from specific parental combinations. Objectives for this study are:

1. To determine elongation values for seven representative upland cotton genotypes with Stelometer and HVI;
2. To conduct a diallel analysis with seven upland cotton genotypes to partition GCA and SCA for fiber elongation using Stelometer and HVI;
3. To determine the correlation between Stelometer elongation and HVI elongation;
4. To conduct a generation means analysis (GMA) using HVI elongation to further dissect gene actions involved in fiber elongation from selected parental combinations.
5. To predict gain from selection and gene(s) responsible for fiber elongation in selected parental combinations.

CHAPTER II

LITERATURE REVIEW

Cotton, a fiber crop

Cotton, a crop grown primarily for its fiber, is considered one the major crops grown in over 50 countries worldwide, with roughly 34 million ha (Smith, 1999). As of 2008, world cotton production was about 26 million metric tons with an average yield of 787 kg ha^{-1}. Major cotton producing countries include: China, U.S., India, Pakistan, Uzbekistan and Brazil. There are currently about 50 identified cotton species but only three are grown commercially: *G. arboreum* (diploid), *G. hirsutum* (tetraploid) *and G. barbadense* (tetraploid) (Khadi et al., 2010). The diploid species has 26 chromosomes while the tetraploid species have 52 chromosomes. Doubling of chromosomes happened roughly 1 to 2 million years ago via polyploidization between an African species with an American species, creating the present day "New World" tetraploid species (Wendel et al., 1992; Wendel and Cronn, 2003). *Gossypium hirsutum*, a new world tetraploid, is considered to be the most economically important cotton species due to its high yield potential, good fiber properties and large hectarege grown worldwide (May and Lege, 1999; Meyer, 1974). Crosses made between multiple varieties of upland cotton have created multiple upland races worldwide; these races include: *Palmeri*, *Morilli*, *Richmondii*, *Yucatenanse*, *Punctatum*, *Marie galante* and *Latifolium* (Iqbal et al., 2001 and Khadi et al., 2010).

Cotton fiber classing

Cotton fiber is a variable product. Development of every single fiber on cotton seed is dependent upon growing conditions and genetics as each fiber or seed hair is a single hyper-elongated cell arising from the seed coat (Bradow and Davidonis, 2000). Such variability has mandated a standardized classing system for better precision in measuring fiber properties. The first legislations were the establishment of color and length grades by the U.S. Cotton Futures Act of 1916 and 1918 (Palmer, 1924). Since then, increasing interests from public and private sectors have helped in the development of better testing equipment and standard methodologies for fiber testing. There are three ways cotton fibers can be classified: single fiber properties, bundle fiber properties and yarn properties. The ultimate goal of all these methods is to serve as predictors for the actual manufacturing performance of cotton fibers in the textile industry. Yarn quality classification is undoubtedly the best predictor for processing quality but is also the most time consuming and costly (May and Jividen, 1999). Single fiber testing may serve as a good alternative, but the low speed of testing and the need to perform hundreds of tests for a good representation restricts its usage in an industrial setting (Cui et al., 2003; Sasser et al., 1991). Hence, fiber bundle testing may be the only low cost and feasible method to acquire fiber information for the industry's needs.

In the U.S., the USDA classing office has identified certain fiber traits to be of economic importance, these include: fiber length, length uniformity, strength, micronaire, color and trash content (Smith et al., 2008b). Traditionally, most of these classifications were made subjectively, then by single instruments. But, due to the

increased cotton production in the U.S., and to ensure short turn-around time between farm-gate and textile manufacturers, the cotton industry demanded a more streamlined testing instrument to replace human classers. Joint efforts between the Plains Cotton Cooperative Association (PCCA, 2012) and the Motion Control Inc. had resulted in the concept of High Volume Instrument (HVI) in the 1960s. The first generation HVI allowed for multiple fiber traits to be tested simultaneously within a few minutes and with improved precision. By the early 70s, with initiatives by the USDA, HVI systems had begun to replace human classers at many of the classing offices throughout the U.S. cotton belt. By 1991, HVI fiber strength classing was mandatory for every cotton bale produced in the U.S. for loan purposes by the Commodity Credit Corporation (Ramey, 1999).

Fiber elongation

Materials have the tendency to deform when stress is applied, cotton fiber is no exception. Under ideal condition, cotton fibers, just like many other materials, should be able to stretch when stress is applied and return to the original state once stress is removed, given that the elastic limit is not breached (Riley, 1997). However, the elongation property of plant cell walls, i.e., cotton fiber, is limited and dependent on the frequency and amount of stress applied over time and may deform due to material fatigue (Preston, 1974).

Fiber elongation is a trait commonly reported while obtaining fiber bundle strength (Hertel, 1953). Elongation, measured in percentage, is the ratio of elongated

length and initial length. Currently, fiber elongation values are classified into five different categories: very low (<5.0%), low (5.0%- 5.8%), average (5.9%- 6.7%), high (6.8%- 7.6%) and very high elongation (>7.6%) (Cotton Incorporated, 2012). Over the years, multiple studies on fiber elongation have proposed that fiber elongation contributes, to a varying degree, to the overall yarn quality in upland cotton (Faulkner et al., 2012; Liu et al., 2001; Liu et al., 2005; May and Taylor, 1998). High variations in single fiber elongation could potentially reduce yarn strength up to 46%, whereas low variations in elongation may result in finished yarn to have strength values closer to the combined individual strength and hence, a stronger yarn (Liu et al., 2005; Suh et al., 1993, Suh et al., 1994).

Fiber bundle elongation can be measured using the HVI system or the Stelometer. It has long been hypothesized that fiber elongation, although frequently underutilized, may influence yarn work-to-break. According to Benzina et al. (2007), work required to break a fiber bundle is determined by the area under the curve of load vs. elongation or the stress-strain curve. Work-to-break is a more accurate method of determining spinning performance as it captures total force required to rupturefiber bundle, which is a function of strength and elongation combined. From a manufacturing stand point, elongation is especially important in three processing steps where weak and low elongation fibers tend to break. These steps are ginning, carding and weaving. According to the review by May (1999), elongation has never been a primary emphasis in most cotton breeding programs, but this phenomenon may change quickly due to interest arising from spinners and manufacturers. Besides, a recent study by Faulkner et

al. (2012) using 76 commercially grown cotton cultivars found that fiber bundle elongation is highly correlated with yarn work-to-break, which is indicative of yarn processing performance.

HVI elongation

Since the 1980s, HVI measurement has been used to determine quality traits of cotton bales produced in the U.S. due to the high speed and low cost of testing. HVI elongation, although typically reported along with HVI tenacity, is less utilized than expected (Riley, 1997). Elongation values from HVI are usually thought to be inconsistent and correlate poorly to yarn elongation. To date, there is no standard cotton available to calibrate HVI machinery for elongation, which means that elongation values could fluctuate between systems.

However, the true problem with HVI elongation may lie within the instrumental design of many HVIs. According to a study by Bargeron (1998), instrumental flaws are present in elongation measurement on many of the current HVI systems. The issue has been overlooked due to the high cost of modifying HVI systems and the lack of incentives for fiber elongation improvement. On some older HVI systems, considerable deflection occurs on the metal beams connecting the drive motor to the fiber jaws used to break fibers. Severity of deflection often depends on the strength of the fiber sample tested. When strong cotton samples were used on these flawed systems, total displacements caused by deflection were reported to be almost twice the breaking elongation. Such overestimation of fiber elongation could render these HVI elongation

values meaningless (Bargeron, 1998). However, according to Riley (1997), the efficacy of HVI elongation can be improved with modifications on the HVI software to compensate for material deflections. Using USDA crop samples from 1990 to 1994, the modified HVI software has provided better predictions for yarn elongation than the Stelometer elongation.

Stelometer elongation

The Stelometer is an improved version of the Pressley strength tester (first invented in 1942 to measure only fiber bundle strength) (Pressley, 1942). Patented by Hertel (1955), the Stelometer allows testing of fiber strength and flat-bundle elongation using a weighted pendulum which applies a constant rate of load to break fibers. Since its introduction, Stelometer has been used widely to measure fiber bundle elongation and strength in many cotton genetic studies and cultivar development programs (May and Taylor, 1998; May and Jividen, 1999; Miller and Rawlings, 1967; Scholl and Miller, 1976; Shofner et al., 1991, Thibodeaux et al., 1998). To date, the Stelometer is the only instrument with available standards to calibrate fiber bundle elongation (USDA, 2013). Hence, it is commonly used to compare elongation measurements with the HVI and other fiber testing methods (Sasser et al., 1991; Thibodeaux et al., 1998). According to May and Jividen (1999), heritability estimates by Stelometer for fiber elongation are higher than those on the HVI, especially in advanced generations suggesting better accuracy and ability to separate small differences by the Stelometer.

To measure fiber strength and elongation, there are two commonly used clamp spacer distances or gauge lengths [3.2 mm (1/8 inch) gauge and 0.0 mm gauge]. According to a study by Egle and Grant (1970), strength and elongation of 52 fiber samples from four cotton species vary due to the natural crystalline structure and spiral alignments. The frequency of "structural reversal" (change in spiral orientation of fibrils) is species dependent, which necessitates proper gauge length for testing each species. Comparing bundle strength between the two gauges, fiber bundle strength tested on the higher gauge tends to have a better correlation with yarn and single fiber data as it accounts for the presence of "weak spots" on fiber shafts caused by structural reversals (Orr et al., 1955; Orr et al., 1961). Ramey et al. (1977) have indicated that the 0.0 mm gauge tends to overestimate fiber strength and cause reduction in correlation to yarn tenacity. However, the effect of higher gauge length is less significant for fiber bundle elongation. Due to the emphasis on bundle strength by the industry, elongation measurement on the Stelometer has adopted the 3.2 mm gauge system to better accommodate the strength test.

Qualitative versus quantitative traits

In plant breeding, the genetic control of phenotypic traits is divided into two groups, i.e., qualitative and quantitative traits. Qualitative traits are governed by one or a few genes and expression is discrete, and with little or no environmental impact on expression. Selection for qualitative traits can be conducted with minimal efforts and the inheritance of qualitative traits typically follows the segregating ratio of 3:1 for one gene

and 9:3:3:1 for two genes (Fehr, 1991). However, the majority of plant traits are quantitative and they do not follow the simple expression patterns of qualitative traits. Phenotypic expressions of quantitative traits are often continuous due to contributions from multiple genes and are more sensitive to environmental changes. To distinguish between different levels of quantitative expressions, plant breeders use statistics (means, variances, covariances, regressions and correlations) to quantify the degree of similarity or dissimilarity among individuals (Kearsey and Pooni, 1996).

Variances

According to Falconer (1960), the study of quantitative genetics in crop research is the study of variations among individuals and how one could partition the variations observed into different causes, e.g., variation due to phenotype, genotype, environment, and their interactions. Such variations are quantified mathematically and defined by their respective variance components.

Phenotypic variance is the sum of two variance components, i.e., the genetic or genotype variance and the non-genetic variance. Under the genetic variance, variation observed can be further partitioned into additive variance (breeding value), dominance variance and epistatic variance. For a quantitative trait, breeding value is determined by adding the average effects or contributions of all alleles involved in the trait of interest whereas dominance deviations would be any residual values that cannot be accounted for by the average effects (Bernardo, 2002; Moll and Stuber, 1974). In a breeding population, genotypic variance among individuals can be determined using the formula:

$$\sigma^2_g = \sigma^2_A + \sigma^2_D + \sigma^2_I$$

Where σ^2_g is the total genotypic variance, σ^2_A is the additive variance, σ^2_D is the dominance variance and σ^2_I is the variance of interaction deviations or epistatic interactions (Falconer, 1960; Fehr, 1991).

In crop breeding, regardless of self or cross- pollinated species, additive variance is typically far more important than the dominance variance (Moll and Stuber, 1974). For example, in a cross pollinated species like maize, Hallauer and Miranda (1988) have summarized that additive variance is about 67% greater than the dominance variance for grain yield in 99 distinctive maize populations. For self-pollinated species such as cotton, the proportion of additive variance to total phenotypic variance for fiber traits such as strength, length, elongation and uniformity index were on average, two to three fold greater than the proportion due to dominance variance in the F_2 hybrids of eleven distinctive parents (Jenkins et al., 2009). Berger et al. (2012) observed that the amount of variation in fiber traits explained by general combining ability (indicative of additive variance) far outweighs the specific combining ability (indicative of dominance variance) in a diallel study with eight distinctive parents.

Epistasis

Epistasis is the inter-allelic interactions between two or more loci that control the expression of a trait (Fehr, 1991). In quantitative genetics, epistasis occurs when the simple additive-dominance model fails to explain a majority of variations observed within a population and factors such as maternal effects, reciprocal effects and genotype

by environment interaction are ruled out. In an F_2 generation, epistatic effects can cause phenotypic deviations from the common 3:1 or 9:3:3:1 ratio. Depending on the types of epistasis, expected F_2 phenotypic ratios can be 9:7 or 15:1 for the more common complementary and duplicate epistasis, respectively, and 9:3:4 and 12:3:1 for the less common recessive and dominant epistasis, respectively (Kearsey and Pooni, 1996). For a polygenic trait, one also could expect different allelic distributions among parents which would result in varying degrees of genotypes among progenies. Such variation in allelic distribution is known to affect genetic parameters used to estimate epistasis. Classical models commonly assumed the ideal condition of two loci in a bi-parental cross and all genes having equal effects. Epistasis would be in full association if allelic structure is AABB in one parent and aabb for the other parent and in full dispersion if allelic structures are AAbb and aaBB for the two parents, respectively. However, such conditions are rare and epistasis usually contains some levels of association and dispersion depending on the number of genes, and individual gene effects are hard if not impossible to determine (Kearsey and Pooni, 1996; Mather and Jinks, 1977).

To properly interpret the presence and absence of epistasis in a population, scaling tests are commonly used to test the adequacy of the simple additive-dominance model versus the more complex additive-dominance with epistasis model (Hayman and Mather, 1955; Mather, 1949). General assumptions of the scaling test are: (i) additivity of gene effects, and (ii) no interaction between the heritable (genetic) component and the non heritable component (non-genetic) (Singh and Chaudary, 1977). When fitting data to scales, an additive-dominance model is considered adequate in explaining variations

observed if scales equal zero within their respective standard errors. In the event of inadequacy of additive-dominance model, additional parameters, i.e., epistatic components may be incorporated to better fit the data to the genetic model (Mather and Jinks, 1977).

Environment

The non genetic factors (environment) have the potential of affecting trait performance, more so for quantitative traits than qualitative traits. To minimize the errors due to environments, breeders tend to conduct experiments over multiple locations, replications or years to ensure good performance of potential cultivars (Bernardo, 2002). Under undesirable environments, good genotypes may be overlooked whereas poor genotypes may be rated higher than under favorable conditions. For many quantitative traits, effective selections can be hindered by the interactions between genotypes and environments (G x E). For many breeders, a superior cultivar should always possess minimal G x E, which is indicative of superior adaptability over large geographic areas.

In cotton, the effect of G x E varies among fiber traits, which means that certain fiber traits are more sensitive to environmental changes than others. For example, the portion of sum of squares due to G x E in twelve environments for eight upland cultivars were 8%, 20%, 8%, 8%, 24%, 9% and 3% for lint yield, lint percent, fiber length, strength, uniformity index, micronaire, and elongation, respectively (Campbell and Jones, 2005). While comparing the effect of G x E of cotton yield component versus

fiber quality traits, Geng et al. (1987) have summarized that fiber quality traits are less responsive to environmental changes than yield. Many breeding studies on fiber quality traits in upland cotton have determined that the G x E variance component, especially for fiber elongation, is relatively small in comparison to the genetic factor. These findings are indicative of a strong genetic basis for fiber elongation (Braden et al., 2009; Campbell and Jones, 2005; Cheatham et al., 2003; Green and Culp, 1990; May, 1999; Miller and Rawlings, 1967; Scholl and Miller, 1976).

Heritability

According to Lush (1945), all trait expressions are determined by both heredity and environment and they are the results of interactions between the two components. Heritability estimates vary for traits within the same population and for the same trait across populations. Broad sense heritability (H^2), is comprised of the variation due to genotype (V_G) divided by variation due to phenotype ($V_G + V_E$), where V_E is the environmental variance (Bernardo, 2002; Kempthorne, 1957). In genetic studies, H^2 can be increased by decreasing the V_E, i.e., by having a uniform testing environment, or by increasing the V_G, i.e., using diverse genetic materials. Ultimately, heritability estimates allow breeders to formulate the amount of desirable traits to be expressed in the subsequent filial generations and to gain insights into the probability of successful selections. As mentioned in the previous section, V_G can be further partitioned into V_A (additive variance),V_D (dominance variance) and V_I (Epistatic variance). For many cultivar development programs, narrow sense heritability (h^2) is more useful as it

measures the amount of heritability due to additive effects, which can be captured easily and transmitted to the next generation (Fehr, 1991).

May (1999) has indicated that additive gene effects were predominant for fiber elongation in ten of twelve genetic studies on fiber properties conducted between 1961 and 1994. High levels of additive gene effects for fiber elongation signify the importance of narrow sense heritability. May reported narrow sense heritability for fiber elongation in these studies to range from 0.36 to 0.90. According to Ramey and Miller (1966), additive gene effects for fiber elongation far outweigh the dominance effects in upland cotton, which again, emphasized the importance of narrow sense heritability in cotton fiber traits. While comparing heritabilities for various fiber properties in crosses between commercial cultivars and non-cultivated race stocks, narrow sense heritability for fiber elongation was reported as 0.43, with the additive gene effects component explaining 87% of total genetic variation (Wilson and Wilson, 1975).

Genetic gain

In breeding, genetic gain involves the estimation of selection progress within a given environment or a set of environments when proper selection methods are applied. Due to the polygenic nature of quantitative traits, classification and selection for individual genes cannot be carried out with ease. Instead, selections typically are performed via metrical measurements which involve statistics such as means and variances. A basic assumption is that the phenotype and genotype must correlate well in order for selection to be meaningful. The extent to which superior traits are transferred

from parents to offspring depends heavily on the heritability as high heritability would confer higher occurrence of selected traits in the filial generation and vice versa. For a normally distributed population, a selection differential (k) can be derived from area under the normal curve based on the standard deviation units (Bernardo, 2002; Falconer, 1960; Hallauer and Miranda, 1988).

As indicated by Schwartz and Smith (2008), among nine representative modern and obsolete cultivars since 1922, average means for fiber elongation have decreased in modern cultivars since the 1960s. Such decrease in elongation may have been due to the heavy emphasis on fiber strength and length traits, which have been reported previously to be negatively correlated with elongation (Green and Culp, 1990; Meredith et al., 1991). However, when considering the lack of genetic gain in fiber elongation in commercial cotton cultivars, one must also consider that elongation was hardly a breeding objective for many breeding programs in the U.S. (May, 1999). Since the wide spread use of HVI for fiber testing in the 80s, the validity of elongation values reported in genetic studies may be questionable due to the lack of calibration (Bargeron, 1998).

Effective factors

The term "effective factor" was introduced by Mather (1949) to estimate the number of segregating genes between two lines. Since then, the concept was further discussed and elaborated by many authors such as Falconer (1960), Lande (1981), Wright (1968) and Mather and Jinks (1977). As the understanding of quantitative genetics grew, effective factors were later described as "number of loci" and were used

primarily to estimate the number of loci responsible for expression of quantitative traits (Falconer, 1960). The principle behind Falconer's estimation of effective number of loci is based on the idea that for a given amount of phenotypic variation, the amount of responses is proportionate to the number of loci involved, and genes with larger effects may produce larger responses with a smaller number of genes. However, it is unlikely that such effect can be measured on an individual gene basis. Gene linkage may also skew the total responses or phenotypic variations observed, and there is no definite way of determining the amount of linkage in a given population.

Mather and Jinks (1977) described effective factors as a linked group of genes responsible for trait expression in crosses between two true-breeding lines. Validity of estimation relies on four assumptions: (i) no epistatic interactions between alleles; (ii) genes of equal effects; (iii) complete association of like alleles; and (iv) no linkage between genes. In quantitative genetics, effective factors represent areas in the chromosome of polygenic systems where their genetic contents may change and evolve. In contrast with regular genes where changes can happen only through mutations, expressions of effective factors are dynamic. These factors may be re-assorted via recombination which could alter expressions, and they may also be interspersed with gene(s) from another polygenic system so expression of one polygenic system may affect another. Over time, quantification of these factors may help breeders to better understand polygenic variability in breeding populations and their responses to selections (Mather, 1973). Overall, all the models derived to estimate effective factors are slightly different in terms of their idealistic scenarios and assumptions. Each model

has its own advantages and disadvantages but no one model is superior to another. Although the estimations of effective factors may appear to be crude, they may still serve as predictors for the number of genes or loci and the range of additive genetic variance or polygenic variability for a specific trait in the population.

Effective factors have been successfully used in multiple crops to estimate polygenic variability and number of factors or loci in various agronomic crops, e.g., corn [*Zea mays*] (Dudley and Lambert, 2004; Toman Jr. and White, 1993), cowpea [*Vigna unguiculata* (L.) Walp] (Nzaramba et al., 2005; Tchiagam et al., 2011), and cotton [*Gossypium hirsutum*] (Luckett, 1989; Singh et al., 1985; Verhalen et al., 1970; Zhang et al., 2007). Based on estimates by Al-Rawi and Kohel (1970), the number of effective factors for fiber elongation in crosses between nine representative upland genotypes were between 3 and 4 in comparison to 1 to 2 for 2.5% span length and strength, which is indicative of a larger genetic variability governing fiber elongation.

Statistical design for crop improvement

Diallel analysis

Diallel is a commonly used mating design in the study of quantitative inheritance to estimate GCA and SCA. Diallel was first coined by Griffing (1956a) and since then; many breeders have utilized this method for crop improvement due to the versatility and ease of use as an unlimited number of parents can be included as long as resources permit (Griffing, 1956a; Griffing 1956b). Depending on the needs and experimental design, there are four commonly used diallel methods: (I) parents with F_1 and reciprocal

included; (II) parents and F_1; (III) no parents but F_1 and reciprocals included; and (IV) only F_1 included. Also, there are two models for each of the methods depending on the experimental assumptions. Model I assumes genotype and block effects to be fixed while model II assumes genotype to be variable and block effects fixed (Griffing, 1956b). Genetic variation is classified into half-sib and full-sib based on variation among crosses. Half-sib variation is the variation due to additive gene action (GCA) and is estimated by the contribution of a specific parent to the overall mating population. Full-sib variation is the variation due to dominance gene action and is estimated via variation due to specific cross involving two parents (SCA). Both half-sib and full-sib estimations assume negligible epistatic interactions (Bernardo, 2002; Fehr, 1991).

As for cotton, although sold primarily as cultivars, it is still quite common for the diallel design to be used as a mating design due to cross compatibility, both inter and intra-species, and the ease to obtain homozygous lines via selfing. In fact, diallel is commonly used to investigate heritability and specifically the GCA component of lint yield, lint percent and various fiber quality traits with economic importance such as length, strength, micronaire, elongation, etc. (Al-Rawi and Kohel, 1970; Ali et al., 2008; Berger et al., 2012; Braden et al., 2009; Cheatham et al., 2003; Lee et al., 1967; Pavasia et al., 1999; Verhalen et al., 1970). For diallel analysis to be valid, several assumptions must be met: (i) diploid segregation, (ii) homozygous or inbred parents, (iii) no reciprocal differences, and (iv) no genotype by environment interactions. According to Endrizzi (1962) and Kimber (1961), upland cotton is a unique allopolyploid which segregates in a diploid fashion. Homozygous parents in cotton are easily obtainable via

natural selfing in the absence of insect pollinators. Previous studies in upland cotton have indicated that reciprocal effects are insignificant (White and Kohel, 1964; Al-Rawi and Kohel, 1969). As for the genotype by environment interactions, this assumption can be tested using standard statistical measures and partitioned accordingly.

According to several diallel studies on fiber elongation in upland cotton, GCA effects were more profound and meaningful than SCA (Anguiar et al., 2007; Green and Culp, 1990; Jenkins et al., 2009; Lee et al., 1967). For many cultivar development programs, SCA is utilized rarely due to the high production cost for hybrid cotton seeds. However, Cheatham et al. (2003) reported significant SCA effects in fiber elongation, micronaire and length in upland cottons in crosses between U.S., Australian and wild cottons and suggested that considerable gains could be made via SCA in these diverse materials. In a diallel analysis of eight extra long staple (ELS) type upland cottons, GCA was observed to be more stable across years in comparison to the SCA effects, especially for fiber strength, length and uniformity (Berger et al., 2012).

Generation means analysis

Generation means analysis is a method commonly used to dissect gene action in quantitative traits for breeding purposes. Mather (1949) was the first to introduce generation means analysis as a biometrical tool to partition gene inheritance into additive, dominance and epistatic effects (additive x additive, additive x dominance, and dominance x dominance), and the concept was further discussed and elaborated by Anderson and Kempthorne (1954), Gamble (1962), Hayman (1958), Hayman (1960),

and Mather and Jinks (1982). In crop improvement, proper understanding of the various genetic controls for quantitative traits are undeniably important, and may help in maximizing breeding gains with minimal efforts. The estimation of genetic effects using generation means is more robust than the use of variance components (V_A, V_D, and V_I) due to: (i) the inherently smaller sampling error when genetic effects are estimated using means; and (ii) the least squares method is biased towards V_A and often minimizes contribution of V_D due to regression-fitted values (Bernardo, 2002). To estimate the six parameters in generation means analysis (*m, a, d, aa, ad,* and *dd*), there are six basic generations needed. These generations are: two homozygous parents or inbred lines, F_1, F_2, and two backcross generations generated by crossing the F_1 to the respective parents (Kearsey and Pooni, 1996).

For quantitative traits, estimation of gene contribution at a single locus level would be unfeasible and meaningless. Instead, the pooled effects of all loci or means are more suitable for use in estimating gene effects and epistatic interactions (Hayman, 1958). In general, there are three possible genetic systems or scenarios in generation means analysis with each having its own implication and justification for additive, dominance and epistasis *per se*. These three scenarios are: (i) significant additive-dominance without epistasis (or ignored), (ii) significant additive-dominance and less important but significant epistasis, and (iii) significant additive-dominance and epistasis, all with equal importance. When epistasis is minimal or non-significant, validity of additivity and dominance of quantitative trait should be unbiased. However, when

epistasis is significant and important, i.e., in group (iii), efficacy of the additive-dominance effects may be limited (Hayman, 1960).

Genetic controls for fiber traits have been studied extensively in upland cottons. The majority of fiber elongation studies, performed with either HVI or Stelometer, have concluded that the additive component is more important than the non-additive components (Al-Rawi and Kohel, 1970; Ali et al., 2008; Aguaiar et al., 2007; Berger, et al., 2012; Cheatham et al., 2003; Green and Culpl, et al, 1990; Jenkins et al., 2009; Lee et al., 1967; Tang et al., 1993). In contrast, a study by May and Green (1994) reported significantly higher dominance gene effects than additive effects in fiber elongation in elite Pee Dee germplasm lines. Probable cause for this is the continuous selection in the narrow gene pool of Pee Dee lines for more than 40 years which causes depletion in total fixable genetic variance. In a separate study consisting of 64 commercial F_2 hybrid cotton cultivars, dominance gene effects was determined to be more prominent than additive gene effects in fiber elongation and a few other important fiber traits (Tang et al., 1996). This means that for hybrid production, although relatively rare in the U.S., dominance gene effects may remain an important factor to consider.

CHAPTER III

DIALLEL ANALYSIS FOR FIBER ELONGATION

Plant materials

A total of seven upland cotton genotypes with distinctive fiber properties were selected for this study. These genotypes were: TAM-B-182-33 (TAM), ST4498-B2RF (STO), UA 48 (ARK), PSC 355 (PSC), Acala 1517-99 (ACA), MD-9 (MD9) and Dever (DEV). Pedigrees of all genotypes are summarized in Table 1.

Material and methods

Early screening and generation development

The seven selected genotypes were grown under greenhouse culture during the fall of 2009 at Texas A&M University (TAMU), College Station, TX. Ten plants per genotype were tagged individually for tracking purposes. At flowering, filial one (F_1) seeds were generated via crossing of all parental genotypes in all possible combinations disregarding reciprocals. A total of 21 F_1 combinations were created and each cross made was traceable to specific parental plants.

Table 1. Pedigrees of parental genotypes for diallel analysis.

Genotype	Pedigree
TAM-B-182-33	PI 654362. An extra long staple upland type cotton developed at Texas A&M University, College Station, TX. Recommended for production in central and south Texas due to longer maturity. Excellent fiber length (>32.0 mm) and bundle strength reported by HVI. It is a cross between: TAM 94L- 25 (Smith, 2003) and PSC 161 (May et al., 2001). TAM 94L- 25 (PI 631440) is a breeding line with early maturity and high length and strength. PSC 161 (also known as GA 161, PI 612959) is a released cultivar with high yield potential and good fiber properties for Georgia and South Carolina (Smith et al., 2009).
ST4498-B2RF	PVP 200800230. U.S. patent pending 61/197,375. This is a high yielding cultivar with good fiber properties developed by Bayer CropScience. The agronomic properties of ST4498-B2RF are similar to ST 457 (PVP 200200277). It contains resistance to insect pests such as cotton bollworm, cotton leafworm, fall armyworm, pink bollworm and tobacco bollworm. It also carries resistance to the herbicide glyphosate.
UA 48	PI 660508 PVPO. Also known as UA48, this is a cultivar developed by Arkansas Experimental Station. Has comparable yield to commercial check DP 393 when grown in northern locations. Possesses early maturity, good fiber properties, highly resistant to bacterial blight caused by *Xanthomonas campestris* and good resistance to Fusarium wilt. Parents include Arkot 8712 and FM 966. Arkot 8712 (PI 636101) is a cultivar adapted to northern Arkansas with good yield potential and fiber properties. FM 966 (PI 619097 PVPO) is a cultivar developed by CSIRO, Australia (Bourland and Jones, 2012).
PSC 355	PI 612974. This is a cultivar developed by Mississippi Agricultural and Forestry Experimental Station and licensed to Phytogen Seed Company, LLC. Commonly used as a commercial check due to good yield potential, good maturity, good agronomic properties and consistently high elongation in comparison to many other commercial checks in both irrigated and non-irrigated trials (Benson et al., 2000).

Table 1. Continued.

Genotype	Pedigree
Acala 1517-99	PI 612326, PVP 200000181 (Cantrell et al., 2000). Developed by New Mexico State University, NM as a high length cultivar averaging 31mm for 2.5% span length and high lint percent. Originated from single plant selection from experimental B2541, derived from cross between B742 and E1141. B742 is derived from Acala 9136/250. Parents of E1141 are unknown.
MD-9	PI 659507. Non commercial breeding line developed by USDA-ARS, Stoneville, Mississippi. It is a nectariless line with superior resistance to Lygus infestation for the Mid South Cotton growing region. Possesses good combining ability for yield and fiber length and strength. Parents include a strain from MD51ne and MD15. MD51ne (PI 566941) is a high strength strain derived from species polycross. MD15 (PI 642769) is a nectariless cotton line with superior fiber properties (Meredith and Nokes, 2011).
Dever	Unreleased experimental line from Texas A&M AgriLife Experimental Station, Lubbock. Pedigree consists of FM 956 (PI 619096) and FM 958x{[(EPSM 1667-1-74-4-1-1xStahman P)xMexico-CIAN-95]x[EPSM 1015-4-74xEPSM 1323-3-74]}

Selfed seed were collected from each parental plant from flowers not used for crossing since cotton is self pollinated in the absence of insects, especially bumble bees (*Bombus spp.*) and honey bees (*Apis spp.*). At harvest, all selfed bolls were bulked by individual plants and all crosses were harvested individually. Samples were ginned on a laboratory saw gin and fiber samples were analyzed at the Fiber and Bio-polymer Research Institute (FBRI), Lubbock, TX. Elongation values were determined using the Stelometer 654® (Uster, 2012b) under controlled environmental conditions at the FBRI (65% relative humidity, ± 1%; and 21°C ± 1°C) for all parental materials. Parental plants

with elongation values more than two standard deviations away from the genotypic mean of all parental plants within each genotype, along with their corresponding F_1 combinations, were excluded from the study in an effort to maintain genetic purity. Elongation values for parental materials used in this study are summarized in Table 2. Selected parental and F_1 seeds were used for summer planting in 2010 in the field at the Texas A&M AgriLife Research Farm, College Station, TX.

Table 2. Elongation prescreening for seven parental genotypes using Stelometer.

Parents:	Elongation (%)
Dever	8.6 ± 0.3
PSC 355	8.5 ± 0.7
ST4498-B2RF	8.4 ± 0.5
MD-9	8.2 ± 0.4
Acala 1517-99	7.0 ± 0.7
TAM-B-182-33	6.3 ± 0.2
UA 48	6.0 ± 0.2

Field study

In 2010 and 2011, a diallel analysis was performed at the Texas A&M AgriLife Research Farm, College Station, TX. All plots were managed using standard cultural practices for cotton production in central Texas including furrow irrigation, fertilization and Texas boll weevil (*Anthonomus grandis* Boheman) eradication program. The study was planted in 8.0 m x 1.0 m plots in the field. At approximately two weeks after

seedling emergence, all plots were thinned to final plant spacing of 0.33 m to 0.50 m to ensure uniform interplant competition. The soil type was Westwood silt loam, a fine-silty, mixed thermic Fluventic Ustochrept, intergraded with Ships clay, a very fine, mixed, thermic Udic Chromustert. All seven parents and 21 F_1 genotypes were grown in a randomized complete block design (RCBD) with three replications in 2010 and four replications in 2011. Seed source of 2010 was generated from the greenhouse in 2009, and seed source for 2011 was generated under field conditions in the 2010 growing season. At harvest, 30 bolls per entry per rep were hand-harvested from the first and second fruiting positions in the middle of the fruiting zone. Samples were ginned on a laboratory saw gin without lint cleaner. Fiber samples were analyzed using HVI and Stelometer at FBRI, Lubbock, TX.

Stelometer analysis

Stelometer 654® (Uster, 2012b) was used to determine elongation (Elo-S) and strength (Str-S) for all diallel entries in 2010 and 2011 under controlled environment conditions (65% relative humidity, ± 1%; and 21°C ± 1°C) at the FBRI, Lubbock, TX. All samples were blended with a tabletop fiber blender to ensure uniformity. Testing was performed using Stelometer clamps with 3.2 mm (1/8 inch) gap according to the American Society for Testing and Materials protocol, publication D1445/ D1445M-12 (ASTM, 2012). Each sample was tested with three replications along with three Stelometer standards C39, L2 and M1 (elongation values of 7.1%, 5.6% and 6.4%, respectively, and strength values of 246.0 kN m kg^{-1}, 176.4 kN m kg^{-1}, and 301.8 kN m

kg^{-1}, respectively) (USDA, 2013). Inclusion of standards allowed for daily elongation and strength drifts to be readjusted using standard regression procedures (Hequet, 2012).

HVI analysis

All entries for diallel analysis were tested with the HVI 1000® (Uster, 2012a) at FBRI Lubbock, TX in a controlled environment (65% relative humidity, ± 1%; and 21°C ± 1°C) for fiber strength (Str-H), upper-half mean length (UHML), micronaire (Mic), elongation (Elo-H) and uniformity index (UI). Two replications were performed for each sample following ASTM protocol, publication D5867– 05 for HVI analysis (ASTM, 2005). Three elongation references for HVI were created following methods previously described by Hequet et al. (2006). References were included during daily analysis to readjust for possible machine calibration drift. To further minimize possible variations in elongation readings, all samples were analyzed on the same HVI 1000® system over the two-year period of the study.

Statistical analysis

Prior to diallel analysis, all fiber data from HVI and Stelometer were tested for residual goodness of fit using Shapiro-Wilk W test in JMP Pro 10 (SAS Institute, 2013). Transformation was performed when necessary to ensure normality of data for analysis.

Diallel analysis

The Proc GLM (General Linear Model) procedure of SAS was used to perform analysis of variance for all fiber properties. Year and entry were considered to be fixed effects and means were separated using Fisher LSD (SAS Institute, 2011). All traits with significant entry by year interactions were analyzed separately. Diallel analysis with no reciprocal (model 1, method II) was used to partition the general combining ability (GCA) and specific combining ability (SCA) for all fiber properties reported by HVI and Stelometer (Griffing, 1956a; Griffing 1956b). Analyses were performed using SAS macro "Diallel-SAS05" as previously reported by Zhang et al. (2005). Estimations of GCA and SCA by Diallel-SAS05 were calculated based on the following models:

$$x_{ij}=u+g_i+g_j+s_{ij}+\frac{1}{bc}\sum_k\sum_l e_{ijkl}$$

$$\begin{aligned} i, j &= 1, \ldots., p, \\ k &= 1, \ldots., b, \\ l &= 1, \ldots., c, \end{aligned}$$

Expected mean squares:

$$\text{GCA} = \sigma^2+(p+2)\left(\frac{1}{p+1}\right)\sum g_i^2 \;;$$

$$\text{SCA} = \sigma^2+\frac{2}{p(p-1)}+\sum_i\sum_j s_{ij}^2$$

Effects estimation:

$$\hat{g}_i = \frac{1}{p+2}[X_{i.} + x_{ii} - \frac{2}{p}X_{..}];$$

$$\hat{s}_{ij} = x_{ij} - \frac{1}{p+2}[X_{i.} + x_{ii} + X_{j.} + x_{jj} + \frac{2}{(p+1)(p+2)}X_{..}]$$

where:

x_{ij}= mean of crossing *i*th and *j*th inbreds, u= population mean; $g_i(g_j)$ = GCA effect; s_{ij} = SCA effect; s_{ij} - s_{jl} and e_{ijkl} are effects specific to the *ijkl*th observation; σ^2 = error; p= number of parents; $\hat{g}_i$= GCA estimation of the *i*th observation; $\hat{s}_{ij}$= SCA estimation of the *i*th and *j*th observations; $X_{i.}$, $X_{j.}$= means of all F_1 combinations with *i* and *j* inbreds, respectively.

Correlation analysis

Correlation analysis was performed on Elo-S, Str-S, Elo-H, Elo-H, UHML, UI and Mic using multivariate analysis procedure in JMP Pro 10 (SAS Institute, 2013). Due to significant entry by year interaction, all traits were analyzed within years.

Results and discussion

HVI

All fiber properties reported by HVI differed ($P \leq 0.05$) in 2010 and 2011 except for UHML and Mic (Table 3). Fiber UI was the only trait with insignificant entry*year interaction, hence, analysis was combined across years. In 2011, parents STO and TAM and all F_1 combinations with STO and TAM as one of the parents were excluded from analysis due to possible seed contamination. Based on the entry means by year (when applicable), Elo-H for all entries improved from 2010 to 2011which suggests that 2011 was a more favorable year (Table 4). Entries varied for all HVI properties but for this study, discussion will focus primarily on Elo-H and factors which may have direct impact on fiber elongation. Due to significant entry by year interaction for Elo-H, UHML, Str-H and Mic, means for 2010 and 2011 were analyzed and reported separately (Table 4). Elo-H of parental genotypes included in this study ranged from 5.3% to 8.3% in 2010 and 7.1% to 9.4% in 2011, which supported the rationale of diversity on fiber elongation for the study. All five parental genotypes with two years of data showed improvement in Elo-H (Table 4).

Significant GCA was reported for all HVI fiber properties in 2010 and 2011. As for SCA, all but Str-H in 2010 and Elo-H in 2010 were significant (Table 5). As expected, GCA for Elo-H exceeded SCA variance by 49 fold and 8 fold, 2010 and 2011 respectively, suggesting a larger additive contribution in fiber elongation which agrees with previous reports (Campbell and Jones, 2005; May and Taylor, 1998; Ramey and Miller, 1966; Quisenberry, 1975). Of the seven parents, PSC and DEV both had

significant and positive GCA estimates in both years for Elo-H, whereas parent MD9 consistently exhibited negative and significant GCA in both 2010 and 2011 (Table 6). TAM and MD9 were selected for their improved length and/or strength characteristics (Meredith and Nokes, 2011; Smith et al., 2009) with no apparent emphasis on Elo-H, thus resulting in poor parental combiners for Elo-H in this study. As expected, PSC consistently exhibits high Elo-H (Benson et al., 2000; Marek and Bordovky, 2006; Smith et al., 2008). Similarly, the experimental line DEV also reported good GCA values which lead to the conclusion that these two genotypes may be good sources for fiber elongation. There is no literature relative to whether or not Elo-H was a selection criteria in the development of PSC but such was the case with DEV (Dever, 2012). Cultivar ARK alternated across years in GCA for Elo-H suggesting that the parent was more susceptible to environmental parameters and may require further investigation. Parent ACA was the only parent with insignificant GCA for Elo-H in 2010 but significantly negative GCA in 2011.

Table 3. Mean squares of combined ANOVA of HVI fiber properties measured in 2010 and 2011 in College Station, TX.†

S.O.V.	Elo-H (%)	UHML (mm)	UI (%)	Str-H (kN m kg^{-1})	Mic (unit)
Year	38.4**	1.3	2.2*	49.9**	0.0
Error A	0.4	1.6	0.5	5.2	0.8
Entry	3.0**	6.8**	1.2**	4.4**	3.4**
Entry*Year	1.1**	4.4**	0.8	16.7**	2.7**
Error B	0.1	0.3	0.4	1.2	0.3

*, ** Significant at 0.05 and 0.01 probability level, respectively.
†Elo-H, HVI elongation; UHML, HVI upper-half mean length; UI, HVI uniformity index; Str-H, HVI strength; Mic, HVI Micronaire.

The SCA estimates for Elo-H were non-significant for 2010 while nine F_1 combinations were significant for 2011. Interestingly, all significant combinations in 2011 exhibited negative SCA estimates for Elo-H except for the STO x ACA combination, which resulted in a significant and positive SCA estimate (Table 7). Given that both STO and ACA exhibited significant and negative GCA estimates of Elo-H in 2011, and that their F_1 Elo-H mean was higher than both parents (Table 4), heterosis may be a good explanation for the F_1 having a positive SCA value of 0.88. The PSC and DEV combination did not achieve significant SCA value for 2011 and even with high positive GCA values for both parents in 2011, the SCA was non-significant. This would be a good indicator that the parents are carrying similar alleles for elongation.

Table 4. Parental and F_1 means of HVI fiber properties measured in 2010 and 2011 in College Station, TX. †

	Elo-H (%)		UHML (mm)		Str-H (kN m kg^{-1})		Mic (unit)		UI (%)
Entry ‡	2010	2011	2010	2011	2010	2011	2010	2011	2010/2011
STO x TAM¶	6.2 h-l§	n/a	31.24 cde	n/a	346.2 f-k	n/a	4.4 fgh§	n/a	84.1c-f
STO x ARK¶	6.6 f-i	n/a	30.23 fgh	n/a	362.9 b-f	n/a	4.8 bc	n/a	84.7 a-e
STO x PSC¶	7.4 bcd	n/a	28.45 klm	n/a	330.3 k	n/a	4.6 cde	n/a	83.3 f
STO x ACA¶	7.4 bcd	n/a	29.21 ijk	n/a	355.7 c-i	n/a	4.4 fgh	n/a	84.6 a-e
STO x MD9¶	6.9 d-g	n/a	29.46 hij	n/a	345.6 f-k	n/a	4.4e-h	n/a	83.9 ef
STO x DEV¶	7.9 abc	n/a	29.72 g-j	n/a	350.5 d-j	n/a	4.5 def	n/a	84.5 cde
TAM x ARK¶	5.4 m	n/a	33.27 a	n/a	357.9 c-h	n/a	4.3 hi	n/a	85.1 abc
TAM x PSC¶	6.3 g-k	n/a	31.24 cde	n/a	344.9 g-k	n/a	4.47d-h	n/a	84.3 c-f
TAM x ACA¶	5.6 lm	n/a	33.27 a	n/a	348.6 e-j	n/a	3.9 k	n/a	84.7 a-e
TAM x MD9¶	5.6 lm	n/a	32.26 b	n/a	346.6 f-k	n/a	3.9 jk	n/a	85.0 a-d
TAM x DEV¶	6.4 f-j	n/a	32.00 bc	n/a	360.6 b-h	n/a	4.0 jk	n/a	84.6 a-e
ARK x PSC	6.6 e-h	7.8 cd	29.72 g-j	30.15 abc	344.9 g-k	392.2 a	5.0 ab	4.7 abc	85.2 abc
ARK x ACA	6.3 g-k	7.2 fg	31.75 bcd	29.72 cde	351.1 d-j	345.9 g	4.3 fgh	4.7 ab	84.2 c-f
ARK x MD9	5.9 j-m	7.7 cde	30.99 def	29.79 bcd	364.9 b-e	354.8 efg	4.5 d-g	4.6 a-d	85.1 abc
ARK x DEV	6.5 f-j	8.5 b	30.99 def	29.65 cde	377.3 ab	361.6 def	4.5 d-g	4.7 abc	85.0 a-d
PSC x ACA	7.3 cde	7.4 ef	28.45 kl	30.23 abc	338.1 ijk	372.0 cd	4.6 cde	4.5 a-d	84.7 a-e
PSC x MD9	6.4 g-j	7.6 de	29.46 hij	30.61 ab	347.6 f-k	378.1 bc	4.6 cde	4.3 efg	85.7 a
PSC x DEV	7.8 abc	9.1 a	29.46 hij	30.02 abc	361.6 b-g	398.4 a	4.5 def	4.2 g	85.2 abc
ACA x MD9	6.0 i-m	7.2 fg	30.48 fgh	30.10 abc	360.9 b-g	349.4 fg	4.1 ij	4.4 def	84.7 a-e
ACA x DEV	6.9 def	7.6 de	30.48 efg	30.10 abc	367.2 bcd	369.9 cd	4.0 jk	4.5 cde	85.1 abc
MD9 x DEV	6.8 d-g	8.0 c	30.99 def	30.40 ab	361.3 b-g	398.2 a	4.3 ghi	4.2 fg	85.6 ab
ACA	6.5 f-j	7.1 g	29.97 ghi	29.08 de	348.2 e-j	366.8 cde	3.9 jk	4.5 bcd	84.6 b-e
TAM¶	5.3 m	n/a	33.78 a	n/a	343.0 h-k	n/a	3.6 l	n/a	84.6 b-e
DEV	8.2 a	9.4 a	29.46 hij	28.88 e	369.2 bc	346.7 g	4.0 jk	4.6 a-d	84.0 def
MD9	5.9 j-m	7.1 g	28.96 jk	30.73 a	337.6 jk	373.9 bcd	4.3 ghi	3.8 h	84.4 cde
PSC	8.0 ab	9.4 a	27.43 m	29.64 cde	308.9 l	387.4 ab	4.9 ab	4.1 g	84.3 c-f
STO¶	8.3 a	n/a	27.69 lm	n/a	345.9 f-k	n/a	4.7 cd	n/a	84.2 c-f
ARK	5.7 klm	9.3 a	31.49 bcd	27.81 f	387.8 a	342.0 g	5.1 a	4.8 a	84.3 c-f
Mean	6.6	8.0	30.43	29.83	352.3	369.2	4.4	4.4	84.7
C.V.	5.9	3.6	1.71	2.01	3.1	2.8	3.1	3.9	0.8

†Elo-H, HVI elongation; UHML, HVI upper-half mean length; UI, HVI uniformity index; Str-H, HVI strength; Mic, HVI Micronaire.

‡ STO, ST4498-B2RF; TAM, TAM-B-182-33; ARK, UA 48; PSC, PSC 355; ACA, Acala 1517-99; MD9, MD-9; DEV, Dever.

§ Mean values followed by the same letter are not different at p <0.05 according to Fisher LSD.

¶ Parent or F_1 with only 2010 data; n/a, data not available.

Table 5. Mean squares of GCA and SCA for HVI fiber properties in 2010 and 2011 in College Station, TX. †

	Elo-H		UHML		Str-H		Mic		UI
	2010	2011	2010	2011	2010	2011	2010	2011	2010/2011
GCA	9.36**	8.42**	4.93**	4.66**	24.97**	25.62**	1.58**	0.80**	1.18**
SCA	0.19	1.04**	0.15**	1.53**	2.1	10.08**	0.03**	0.08*	1.41**

*, ** Significant at 0.05 and 0.01 probability level, respectively.

†Elo-H, HVI elongation; UHML, HVI upper-half mean length; UI, HVI uniformity index; Str-H, HVI strength; Mic, HVI Micronaire; GCA, General combining ability; SCA, Specific combining ability.

Table 6. GCA estimates for HVI fiber properties in 2010 and 2011 in College Station, TX. †

	Elo-H (%)		UHML (mm)		Str-H (kN m kg^{-1})		Mic (unit)		UI (%)
Entry‡	2010	2011	2010	2011	2010	2011	2010	2011	2010/2011
STO¶	0.64**	n/a	-1.10**	n/a	-3.94	n/a	0.15**	n/a	-0.39**
TAM¶	-0.78**	n/a	1.93**	n/a	-3.07	n/a	-0.32**	n/a	0.00
ARK	-0.49**	0.24**	0.72**	-0.54**	12.90**	-10.78**	0.28**	0.22**	0.07
PSC	0.51**	0.38**	-1.25**	0.22	-14.79**	14.34**	0.30**	-0.11**	-0.01
ACA	-0.09	-0.67**	0.00	-0.11	-0.06	-6.31**	-0.21**	0.08*	0.02
MD9	-0.41**	-0.50**	-0.23*	0.55**	-1.94	1.85	-0.06**	-0.21**	0.20
DEV	0.63**	0.48*	-0.08	-0.12*	10.90**	8.86**	-0.13**	-0.03	0.10

*, ** Significant at 0.05 and 0.01 probability level, respectively.

†Elo-H, HVI elongation; UHML, HVI upper-half mean length; UI, HVI uniformity index; Str-H, HVI strength; Mic, HVI Micronaire.

‡ STO, ST4498-B2RF; TAM, TAM-B-182-33; ARK, UA 48; PSC, PSC 355; ACA, Acala 1517-99; MD9, MD-9; DEV, Dever.

¶ Parent with only 2010 data; n/a, data not available.

Table 7. SCA estimates for HVI fiber properties in 2010 and 2011 in College Station, TX. †

	Elo-H (%)		UHML (mm)		Str-H (kN m kg^{-1})		Mic (unit)		UI (%)
Entry‡	2010	2011	2010	2011	2010	2011	2010	2011	2010/2011
STO x TAM¶	-0.33	n/a	0.05	n/a	0.94	n/a	0.15	n/a	-0.12
STO x ARK¶	-0.20	n/a	0.08	n/a	1.63	n/a	-0.01	n/a	0.35
STO x PSC¶	-0.42	n/a	0.35	n/a	-3.34	n/a	-0.23**	n/a	-0.91*
STO x ACA¶	0.21	n/a	-0.23	n/a	7.40	n/a	0.04	n/a	0.37
STO x MD9¶	0.00	n/a	0.43	n/a	-0.83	n/a	-0.04	n/a	-0.52
STO x DEV¶	-0.04	n/a	0.45	n/a	-8.78	n/a	0.12	n/a	0.19
TAM x ARK¶	0.06	n/a	0.09	n/a	-4.14	n/a	-0.08	n/a	0.39
TAM x PSC¶	-0.10	n/a	0.20	n/a	10.49	n/a	0.10	n/a	-0.30
TAM x ACA¶	-0.21	n/a	0.89**	n/a	-0.65	n/a	0.01	n/a	0.08
TAM x MD9¶	0.15	n/a	0.11	n/a	-0.73	n/a	-0.04	n/a	0.15
TAM x DEV¶	-0.06	n/a	-0.29	n/a	0.47	n/a	0.09	n/a	-0.11
ARK x PSC	-0.03	-0.82**	-0.20	0.91**	-5.48	19.51**	0.04	-0.12	0.47
ARK x ACA	0.20	-0.44**	0.67*	0.54	-14.01*	-6.15	-0.12	-0.02	-0.54*
ARK x MD9	0.16	-0.05	0.06	-0.05	1.60	-5.48	-0.10	0.12	0.19
ARK x DEV	-0.28	-0.33*	-0.09	0.48	1.16	2.32	-0.04	0.02	0.20
PSC x ACA	0.21	-0.31*	-0.67*	0.22	0.62	-5.06	0.13	0.14	0.05
PSC x MD9	-0.33	-0.28	0.58	0.01	11.98*	-7.34	0.01	0.15	0.84**
PSC x DEV	-0.01	0.18	0.43	0.10	13.18*	13.94**	-0.02	-0.17*	0.44
ACA x MD9	-0.17	0.30*	0.18	-0.17	10.63	-15.35**	-0.01	0.11	-0.13
ACA x DEV	-0.25	-0.29*	0.11	0.49	3.99	6.17	-0.05	-0.06	0.30
MD9 x DEV	-0.05	-0.04	0.86**	0.34	0.00	26.19**	0.10	-0.04	0.70**

*, ** Significant at 0.05 and 0.01 probability level, respectively.

† Mic, HVI Micronaire; UHML, HVI upper-half mean length; UI, HVI uniformity index; Str-H, HVI strength; Elo-H, HVI elongation.

‡ STO, ST4498-B2RF; TAM, TAM-B-182-33; ARK, UA 48; PSC, PSC 355; ACA, Acala 1517-99; MD9, MD-9; DEV, Dever.

¶ F_1 with only 2010 data; n/a, data not available.

Stelometer

Similar to ANOVA results for HVI fiber properties in Table 3, year and entry terms were significant for Elo-S and Str-S (Table 8). Entries did not respond the same to the two growing environments, years, mandating analysis of Elo-S and Str-S within each year. Means for Elo-S and Str-S in each of 2010 and 2011 are reported in Table 9. The parental genotype with the highest Elo-S in 2010 and 2011 was DEV in 2010 at 7.8 % and PSC in 2011 at 7.9%. The F_1 combination PSC x DEV exhibited the highest Elo-S mean among all F_1s for 2010 and 2011 but was not higher than the high parent value within each year. Overall, Stelometer determined Elo-S and Str-S means (Table 9) were numerically lower than HVI determined Elo-H and Str-H means (Table 4). Such observation agrees with findings from a previous study of May and Jividen (1999) and differences could be due to different genetic properties tested by the instruments as well as the lack/difference in calibrations.

Table 8. Combined ANOVA of Stelometer fiber properties measured in 2010 and 2011 in College Station, TX.†

S.O.V.	Elo-S (%)	Str-S (kN m kg^{-1})
Year	0.7*	7.6**
Error A	0.2	1.0
Entry	3.5**	6.9**
Entry*Year	0.9**	8.9**
Error B	0.2	1.3

*, ** Significant at 0.05 and 0.01 probability level, respectively.
†Elo-S, Stelometer elongation; Str-S, Stelometer strength.

Table 9. Parental and F_1 means of Stelometer fiber properties measured in 2010 and 2011 in College Station, TX. †

	Elo-S (%)		Str-S (kN m kg^{-1})	
Entry ‡	2010	2011	2010	2011
STO x TAM¶	5.3 j-n§	n/a	259.0 g-j	n/a
STO x ARK¶	5.9 f	n/a	248.7 j	n/a
STO x PSC¶	6.5 de	n/a	248.4 j	n/a
STO x ACA¶	5.9 f	n/a	276.7 b-f	n/a
STO x MD9¶	5.9 fgh	n/a	265.9 f-i	n/a
STO x DEV¶	7.0 bc	n/a	252.2 ij	n/a
TAM x ARK¶	4.4 pq	n/a	294.3 a	n/a
TAM x PSC¶	4.9 no	n/a	275.0 b-g	n/a
TAM x ACA¶	4.3 q	n/a	278.6 a-f	n/a
TAM x MD9¶	4.8 op	n/a	287.2 ab	n/a
TAM x DEV¶	5.5 g-l	n/a	283.5 a-e	n/a
ARK x PSC	5.4 i-m	5.6 ef	255.7 hij	286.3 bcd
ARK x ACA	5.3 k-n	4.9 g	281.6 a-f	262.7 fg
ARK x MD9	5.5 h-m	5.8 e	294.8 a	276.6 c-f
ARK x DEV	5.5 i-m	6.4 cd	279.2 a-f	264.4 efg
PSC x ACA	5.7 f-j	5.8 e	267.9 d-i	274.4 def
PSC x MD9	5.7 f-i	5.9 de	267.0 e-i	303.6 a
PSC x DEV	7.4 ab	7.7 a	269.3 c-h	291.9 abc
ACA x MD9	5.1 mno	4.9 g	288.7 ab	278.4 c-f
ACA x DEV	6.4 e	6.0 de	290.2 ab	280.5 cde
MD9 x DEV	5.9 fg	6.0 de	290.3 ab	298.2 ab
ACA	5.7 f-k	5.1 fg	282.3 a-f	301.5 ab
TAM	4.5 pq	n/a	285.9 abc	n/a
DEV	7.8 a	7.1 b	276.5 bf	251.6 g
MD9	5.2 lmn	4.7 g	285.5 abc	301.4 ab
PSC	6.7 cde	7.9 a	242.6 j	292.2 abc
STO	6.9 cd	n/a	259.4 g-j	n/a
ARK	4.9 no	6.9 bc	283.9 a-d	264.0 efg
Mean	5.7	6.0	273.9	281.8
C.V.	4.8	7.3	3.7	4.3

† Elo-S, Stelometer elongation; Str-S, Stelometer strength.

‡ STO, ST4498-B2RF; TAM, TAM-B-182-33; ARK, UA 48; PSC, PSC 355; ACA, Acala 1517-99; MD9, MD-9; DEV, Dever.

§ Mean values followed by the same letter are not different at $p < 0.05$ according to Fisher LSD.

¶ Parent or F_1 with only 2010 data; n/a, data not available.

Diallel analysis of Elo-S and Str-S suggested that GCA and SCA effects were significant in 2010 and 2011 except for Str-S in 2010 (Table 10). Another indication that Elo-H and Elo-S may be measuring different components of the cotton fiber structure is that significant SCA effects were found for Elo-H only in 2011, but SCA determined from Elo-S was significant in both 2010 and 2011 with the genotypes used in this study. Based on the GCA estimates for Elo-S, parental genotypes DEV and PSC both were significant combiners among this set of parents in 2010 and 2011 with values of GCA estimates of 0.85% and 0.59%, respectively, for DEV and 0.37% and 0.65%, respectively, for PSC (Table 11). The Stelometer analysis supports HVI analysis that among this set of parents, both DEV and PSC genotypes are promising sources for fiber elongation. Similarly, genotypes TAM (2010 only) and MD9 (2010 and 2011) both contributed negatively to Elo-S but may serve as potential source for Str-S, especially for MD9, which supports the previously discussed high strength and length nature for these two cultivars. As for cultivar ARK, similar to Elo-H GCA estimates (Table 6), Elo-S estimate was not consistent over years and may require further investigation to elucidate (Table 11). Parent ACA showed significantly negative GCA for Elo-S for both years as compared to only one year for Elo-H.

Six Elo-S SCA combinations were significant for 2010 and two were significant for 2011 (Table 12). All six parental combinations in 2010 did not express significant Elo-H SCA. In the same context, in 2011, only two of the six significant Elo-H SCA combinations (Table 7) were significant for Elo-S (Table 12). Such differences may suggest that the Stelometer may have different discriminating power in measuring fiber

elongation than HVI as suggested by May and Jividen (1999). In 2011, none of the parental combinations with PSC and DEV as either one of the parents reported significantly positive SCA for Elo-S. This may indicate that the positive Elo-S GCA of PSC and DEV were nullified by the negative GCA of the other parents used in the study.

Table 10. Mean squares of GCA and SCA for Stelometer fiber properties in 2010 and 2011 in College Station, TX. †

	Elo-S		Str-S	
	2010	2011	2010	2011
GCA	9.45**	10.68**	25.24**	21.94**
SCA	0.30**	1.23**	1.89	6.18**

*, ** Significant at 0.05 and 0.01 probability level, respectively.
† Elo-S, Stelometer elongation; Str-S, Stelometer strength; GCA, General combining ability; SCA, Specific combining ability.

Table 11. GCA estimates for Stelometer fiber properties in 2010 and 2011 in College Station, TX. †

	Elo-S (%)		Str-S (kN m kg^{-1})	
Entry ‡	2010	2011	2010	2011
STO¶	0.51**	n/a	-13.55**	n/a
TAM¶	-0.84**	n/a	6.43**	n/a
ARK	-0.42**	0.04	3.41	-10.45**
PSC	0.37**	0.65**	-13.68**	7.09**
ACA	-0.19**	-0.63**	6.34**	1.16
MD9	-0.28**	-0.62**	8.14**	9.77
DEV	0.85**	0.59**	2.90	-2.61

*, ** Significant at 0.05 and 0.01 probability level, respectively.
† Elo-S, Stelometer elongation; Str-S, Stelometer strength.
‡ STO, ST4498-B2RF; TAM, TAM-B-182-33; ARK, UA 48; PSC, PSC 355; ACA, Acala 1517-99; MD9, MD-9; DEV, Dever.
¶ Parent or F_1 with only 2010 data; n/a, data not available.

Table 12. SCA estimates for Stelometer fiber properties in 2010 and 2011 in College Station, TX. †

	Elo-S (%)		Str-S (kN m kg^{-1})	
Entry ‡	2010	2011	2010	2011
STO x TAM¶	-0.09	n/a	-7..85	n/a
STO x ARK¶	0.15	n/a	-15.07**	n/a
STO x PSC¶	-0.13	n/a	1.53	n/a
STO x ACA¶	-0.07	n/a	9.94	n/a
STO x MD9¶	-0.06	n/a	-2.70	n/a
STO x DEV¶	-0.05	n/a	-11.04*	n/a
TAM x ARK¶	-0.03	n/a	10.54	n/a
TAM x PSC¶	-0.31*	n/a	8.31	n/a
TAM x ACA¶	-0.37*	n/a	-8.08	n/a
TAM x MD9¶	0.15	n/a	-1.25	n/a
TAM x DEV¶	-0.20	n/a	0.20	n/a
ARK x PSC	-0.26	-1.12**	-7.92	7.78
ARK x ACA	0.15	-0.46*	-2.04	-9.78
ARK x MD9	0.47**	0.30	9.29	-4.60
ARK x DEV	-0.69**	-0.26	-1.05	0.58
PSC x ACA	-0.21	-0.32	1.33	-15.66**
PSC x MD9	-0.08	-0.19	-1.49	4.94
PSC x DEV	0.48**	-0.03	6.15	10.59
ACA x MD9	-0.15	0.12	0.32	-14.34**
ACA x DEV	0.02	-0.03	7.00	5.01
MD9 x DEV	-0.36**	0.03	5.26	14.12*

*, ** Significant at 0.05 and 0.01 probability level, respectively.

† Elo-S, Stelometer elongation; Str-S, Stelometer strength.

‡ STO, ST4498-B2RF; TAM, TAM-B-182-33; ARK, UA 48; PSC, PSC 355; ACA, Acala 1517-99; MD9, MD-9; DEV, Dever.

¶ Parent or F_1 with only 2010 data; n/a, data not available.

Correlations analysis of all fiber properties measured by Stelometer and HVI indicated a strong positive association between Elo-S and Elo-H in 2010 and 2011 with values of 0.85 and 0.82, respectively (Table 13). Strong correlation between Elo-S and Elo-H is a good indication that both Stelometer and HVI are capable of taking repeatable and reliable elongation measurements although reported values may be on different scales. Elo-S was significantly and negatively associated with Str-S, r = -0.40, in 2010 but not in 2011. Elo-S was not significantly correlated with Str-H in either year. Elongation measured on HVI was not correlated with Str-H in either year, but a significant negative correlation with Str-S was found for 2010. Comparisons between elongation and strength using both instruments with the parents used in this study support other reports of weak association between the elongation and strength (Benzina et al., 2007; Green and Culp, 1990). Interestingly, strong negative correlations were observed when comparing UHML with Elo-S and Elo-H over both years of study. One explanation for this would be that longer fibers result in high fiber bundle strength as indicated by the positive correlation between UHML and Str-H and between UHML and Str-S, hence, the association of length and elongation may be an artifact (Table 13).

Table 13. Correlation analysis of fiber properties measured by Stelometer and HVI in 2010 and 2011 in College Station, TX.†

A. 2010

	Elo-S	Str-S	Elo-H	Str-H	UHML	UI	Mic
Elo-S	.	.	.	.	.	.	.
Str-S	-0.40**	.	.	.	.	.	.
Elo-H	0.85**	-0.46**	.	.	.	.	.
Str-H	0.01	0.46**	-0.15	.	.	.	.
UHML	-0.66**	0.45**	-0.74**	0.32**	.	.	.
UI	-0.17	0.35**	-0.25*	0.48**	0.41**	.	.
Mic	0.26*	-0.49**	0.35**	-0.09	-0.49**	-0.06	.

B. 2011

	Elo-S	Str-S	Elo-H	Str-H	UHML	UI	Mic
Elo-S	.	.	.	.	.	.	.
Str-S	-0.16	.	.	.	.	.	.
Elo-H	0.82**	-0.24	.	.	.	.	.
Str-H	0.16	0.54**	-0.07	.	.	.	.
UHML	-0.26*	0.37**	-0.51**	0.55**	.	.	.
UI	-0.10	0.48**	-0.21	0.61**	0.59**	.	.
Mic	-0.15	-0.47**	0.05	-0.43**	-0.43**	-0.29*	.

*, ** Significant at 0.05 and 0.01 probability level, respectively.
†Elo-S, Stelometer elongation; Str-S, Stelometer strength; Elo-H, HVI elongation; Str-H, HVI strength; UHML, HVI upper-half mean length; UI, HVI uniformity index; Mic, HVI Micronaire.

CHAPTER IV

SUMMARY OF DIALLEL ANALYSIS

Based on the diallel analysis of fiber elongation on seven distinctive cotton genotypes with Stelometer and HVI, fiber elongation is governed primarily by additive gene action as reported by previous studies (Jenkins et al., 2009; May and Green, 1994; Miller and Rawling, 1967; Quisenberry, 1975). GCA for Elo-H and Elo-S were highly significant with a much larger contribution than SCA as shown in Table 5 and Table 10. Although elongation means varied between the two instruments, cultivar PSC and the DEV breeding line were two parental genotypes identified by both instruments as superior combiners for fiber elongation in this study; whereas MD9 was a consistently negative combiner (Table 6, Table 11).

A few distinctive F_1 combinations identified significant SCA, suggesting that dominance gene action may contribute to fiber elongation in some cases. A few other F_1 combinations with non-significant SCA in 2010 when measured with HVI were significant when tested with Stelometer. Possible explanations could be that the Stelometer may be more precise and accurate in measuring fiber elongation due to inclusion of elongation standards, or it could be that the Stelometer and HVI were testing different fiber characteristics due to biases on each instrument (May and Jividen, 1999). Stelometer utilizes a combed bundle that removes a high percentage of the shorter (< 12 mm) fiber. Therefore, Stelometer has a high length bias whereas HVI, although still with a slight length bias, would test fibers from a larger length distribution, potentially

influencing machine-measured fiber parameters, including elongation. Effects of different fiber distributions on breaking elongation were previously discussed by Liu et al. (2001) and Liu et al. (2005). Besides, the fiber breaking speed for both instruments are vastly different. As mentioned, Stelometer applies a constant rate of load to break fiber bundle as the HVI would imply a much more abrupt breaking force (up to 20 kg-wt), more than the force needed to rupture the strongest of HVI cotton bundle. Such differences in breaking mechanisms and time-to-break were reported to influence fiber elongation (Bargeron, 1998; Riley, 1997).

Correlation analyses indicated that elongation measured by HVI and Stelometer are highly correlated in this study. Observations by Scholl and Miller (1976) and May and Taylor (1998) on negative correlations between fiber elongation and fiber strength generally were supported with the genotypes used in this study. However, such relationship requires further investigation due to inconsistency when comparing strength and elongation across instruments as previously mentioned. Moreover, based on GCA estimates, some of the parental genotypes were positive combiners for both strength and elongation, e.g., DEV in 2010 and 2011 and PSC in 2011 (Table 6). Breeding for simultaneous improvement of fiber elongation and strength may still be possible with the right parental combinations. Breeding for simultaneous improvement of elongation and UHML may be a greater challenge.

In summary, HVI and Stelometer both have their pros and cons in fiber testing but were both capable of making repeatable elongation measurements in this study. Stelometer may possess a slight advantage over HVI in testing accuracy due to inclusion of elongation standards. Depending on the research needs and the stage of breeding process, the Stelometer may be more suitable for early generation screening due to smaller sample size and the ability to include elongation standards for accurate elongation measurements. However, it would be less desirable in late generations because breeders tend to make more selections, e.g., individual plants, in these segregating populations. Thus the HVI may be a better option for larger populations due to lower cost and higher speed of testing than the Stelometer. However, one must always be aware that without elongation standards or the use of calibration cottons such as in this study, elongation values, although consistent within the same HVI machine, may not be sufficiently accurate across machines and years for genetic gain in elongation.

CHAPTER V

GENERATION MEANS ANALYSIS OF FIBER ELONGATION

Plant materials

Four representative upland genotypes were chosen as parents for this study based on their diverse background and known fiber Elo-H properties. These genotypes were: TAM-B-182-33 (TAM), UA 48 (ARK), MD-9 (MD9) and Dever (DEV). Pedigrees of all genotypes are summarized in Table 14.

Material and methods

Early screening and generation development

From the four selected parental genotypes, six distinctive families were created with each family consisting of six generations: P_1, P_2, F_1, F_2, BCP_1 and BCP_2. Prior to generation development, all parental genotypes were screened for Elo-S using the Stelometer 654® (Uster, 2012b) at FBRI, Lubbock, TX under controlled environmental conditions (65% relative humidity, ± 1%; and 21°C ± 1°C). To ensure genetic uniformity in elongation, all parental plants that were two standard deviations away from the genotypic mean were excluded from the generation development scheme. Seeds for all six generations needed for the 2011 and 2012 field seasons were generated in 2010 and 2011, respectively, at the Texas A&M AgriLife Research Farm, College Station, TX.

Table 14. Pedigrees of parental genotypes for GMA analysis.

Genotype	Pedigree
TAM-B-182-33	PI 654362. An extra long staple upland type cotton developed at Texas A&M University, College Station, TX. Recommended for production in central and south Texas due to longer maturity. Excellent fiber length (>32.0 mm) and bundle strength reported by HVI. It is a cross between: TAM 94L- 25 (Smith, 2003) and PSC 161 (May et al., 2001). TAM 94L- 25 (PI 631440) is a breeding line with early maturity and high length and strength. PSC 161 (also known as GA 161, PI 612959) is a released cultivar with high yield potential and good fiber properties for Georgia and South Carolina (Smith et al., 2009).
UA 48	PI 660508 PVPO. Also known as UA48, this is a cultivar developed by Arkansas Experimental Station. Has comparable yield to commercial check DP 393 when grown in northern locations. Possesses early maturity, good fiber properties, highly resistant to bacterial blight caused by *Xanthomonas campestris* and good resistance to Fusarium wilt. Parents include Arkot 8712 and FM 966. Arkot 8712 (PI 636101) is a cultivar adapted to northern Arkansas with good yield potential and fiber properties. FM 966 (PI 619097 PVPO) is a cultivar developed by CSIRO, Australia (Bourland and Jones, 2012).
MD-9	PI 659507. Noncommercial breeding line developed by USDA-ARS, Stoneville, Mississippi. It is a nectariless line with superior resistance to Lygus infestation for the Mid South Cotton growing region. Possesses good combining ability for yield and fiber length and strength. Parents include a strain from MD51ne and MD15. MD51ne (PI 566941) is a high strength strain derived from species polycross. MD15 (PI 642769) is a nectariless cotton line with superior fiber properties, including elongation (Meridith and Nokes, 2011).
Dever	Unreleased experimental line from Texas A&M Agrilife Experimental Station, Lubbock. Pedigree consists of FM 956 (PI 619096) and FM 958x{[(EPSM 1667-1-74-4-1-1xStahman P)xMexico-CIAN-95]x[EPSM 1015-4-74xEPSM 1323-3-74]}

Field study and fiber testing

The GMA study was conducted in 2011 and 2012 at the Texas A&M AgriLife Research Farm, College Station, TX. All six families were planted in a randomized split block design, four replications each, with generations randomized within each family and families randomized within reps. All plots were managed using standard cultural practices for cotton production in Texas including furrow irrigation, fertilization and Texas boll weevil (*Anthonomus grandis* Boheman) eradication program. Plots were 15.0 x 1.0 m. At approximately two weeks after seedling emergence, all plots were thinned to a final plant spacing of 0.33 m to 0.50 m to ensure uniform interplant competition. The soil type was Westwood silt loam, a fine-silty, mixed thermic Fluventic Ustochrept, intergraded with Ships clay, a very fine, mixed, thermic Udic Chromustert. At harvest, individual plants were hand-harvested. To ensure proper representation of genotypes between the non-segregating and segregating generations, three plants were harvested per rep for each of the P_1, P_2 and F_1 generations, 20 per rep for each of the BCP_1 and BCP_2 and 50 per rep for the F_2 generation, giving a total of 12 plants for P_1, P_2 and F_1, 80 plants for each BCP_1 and BCP_2 and 200 plants for the F_2 generation across four reps.

All samples were ginned on a laboratory saw gin without a lint cleaner. Samples with less than 10 g of fiber were omitted from the study due to the minimum weight requirement for HVI analysis. Samples were analyzed using HVI 1000® (Uster, 2012a) at FBRI Lubbock, TX under controlled environmental conditions (65% relative humidity, ± 1%; and 21°C ± 1°C) following ASTM protocol, publication D5867-05 for HVI analysis (ASTM, 2005). Three elongation standards for HVI were created following

methods previously described by Hequet et al. (2006). Standards were included during daily analysis to readjust for possible elongation drifts. To further minimize possible variations in elongation readings, all samples were analyzed on the same HVI 1000® machine for the entire study.

Statistical analysis

Generation means analysis

The Proc GLM™ procedure from SAS™ was used for analyses of variance for all HVI fiber traits (Elo-H, Str-H, UHML, UI and Mic) collected in 2011 and 2012 in College Station, TX (SAS Institute, 2011). Generations and years were considered fixed effects while replications were random. Means for the six generations within each family were separated using Waller LSD. Traits with significant generation by year interactions were analyzed and reported separately by year.

Generation means and variances are two key components from summary statistics used to estimate gene effects (Mather, 1949; Mather and Jinks, 1977). According to Wright (1968), F_2 variances provide estimation of phenotypic variances and in theory should encompass all variations observed in the six generations required for generation means analysis. Homogeneity of F_2 variances is therefore an important requirement for reliable analysis. The DIST macro from SASQuant 1.3 was used to test for homogeneity of F_2 variance based on Chi-square probability (Gusmini et al., 2007).

The scaling test was used to test for the adequacy of the three parameter model (additive and dominance without epistatic effects) with the assumption of linear

relationships among generation means. The ABCD scaling test was performed on each family where A and B test for the additive by dominance epistatic effects, C tests for dominance by dominance epistatic effects and D tests for additive by additive epistatic effects (Mather, 1949; Pooni et al., 1987):

$$A = 2\,BCP_1 - P_1 - F_1$$

$$B = 2\,BCP_2 - P_2 - F_1$$

$$C = 4\,F_2 - 2\,F_1 - P_1 - P_2$$

$$D = 2\,F_2 - BCP_1 - BCP_2$$

Variance components for ABCD scaling test:

$$V(A) = 4V(BCP_1) + V(P_1) + V(F_1)$$

$$V(B) = 4V(BCP_2) + V(P_2) + V(F_1)$$

$$V(C) = 16V(F_2) + 4V(F_1) + V(P_1) + V(P_2)$$

$$V(D) = 4V(F_2) + V(BCP_1) + V(BCP_2)$$

Standard errors for A, B, C and D were determined via square root of corresponding variances. Adequacy for the three parameter model is determined when each of A, B, C and D is not different than zero and within the confines of corresponding standard errors. Where the three parameter model is proven adequate, the application of the more complex six-parameter model is not required (Mather and Jinks, 1977).

Genetic effects estimates were based on Hayman's model using SASQuant 1.3 by Gusmini et al. (2007) in SAS 9.2 (SAS Institute, 2011). This macro partitions the phenotypic expressions into midparent value, *m*; additive effects, *a*; dominance effects, *d*; additive by additive epistatic effects, *aa*; additive by dominance epistatic effects, *ad*

and dominance by dominance epistatic effects, *dd* (Hayman, 1958; Hayman, 1960). Estimates of gene effects were performed using formulas:

$$m = \mu_{F1}$$

$$a = \mu_{BCP1} - \mu_{BCP2}$$

$$d = -\frac{\mu_{P1}}{2} - \frac{\mu_{P2}}{2} + \mu_{F1} - (4 \times \mu_{F2}) + [2 \times (\mu_{BCP1} + \mu_{BCP2})]$$

$$aa = -(4 \times \mu_{F1}) + [2 \times (\mu_{BCP1} + \mu_{BCP2})]$$

$$ad = -\frac{\mu_{P1}}{2} - \frac{\mu_{P2}}{2} + \mu_{BCP1} + \mu_{BCP2}$$

$$dd = \mu_{P1} + \mu_{P2} + (2 \times \mu_{F1}) + (4 \times \mu_{F2}) - [4 \times (\mu_{BCP1} + \mu_{BCP2})]$$

where:

μ_{P1}, μ_{P2}, μ_{F1}, μ_{F2}, μ_{BCP1} and μ_{BCP2} = means for P_1, P_2, F_1, F_2, BCP_1 and BCP_2, respectively.

Fisher's *t*-test is used by the SASQuant program to test if estimates are significantly different from zero. Degrees of freedom (df)were adjusted according to Gusmini et al. (2007) due to uneven sample sizes between the non-segregating (P_1, P_2 and F_1) and segregating generations (F_2, BCP_1 and BCP_2) and were based on the following formulas:

$$df_m = n_{F2} - 1$$

$$df_a = df_{aa} = df_{ad} = \frac{n_{BCP1} + n_{BCP2}}{2} - 1$$

$$df_d = df_{dd} = \frac{n_{F2} + n_{BCP1} + n_{BCP2}}{3} - 1$$

where:

n_{F2}, n_{BCP1} and n_{BCP2} = number of observations for F_2, BCP_1 and BCP_2, respectively.

Variance and heritability estimates

Variances for each generation within each family were estimated to obtain phenotypic (σ_P^2), environmental (σ_E^2), genotypic (σ_G^2), and additive and dominance variance (σ_A^2 and σ_D^2) following the method as described by Warner (1952) and Wright (1968):

$$\sigma_P^2 = \sigma_{F2}^2$$

$$\sigma_E^2 = \frac{\sigma_{P1}^2 + \sigma_{P2}^2 + (2 \times \sigma_{F1}^2)}{4}$$

$$\sigma_G^2 = \sigma_P^2 - \sigma_E^2$$

$$\sigma_A^2 = (2 \times \sigma_{F2}^2) - (\sigma_{EBCP1}^2 + \sigma_{BCP2}^2)$$

$$\sigma_D^2 = \sigma_{F2}^2 - (\sigma_A^2 + \sigma_E^2)$$

Broad sense heritability (H^2) and narrow sense heritability (h^2) on single plant basis were estimated using formulas described by Warner (1952) and Fehr (1991):

$$H^2 = \frac{\sigma_G^2}{\sigma_E^2 + \sigma_G^2}$$

$$h^2 = \frac{2(\sigma_{F2}^2) - (\sigma_{BCP1}^2 + \sigma_{BCP2}^2)}{\sigma_{F2}^2}$$

where:

σ^2_G = genotypic variance; σ^2_E = environmental variance; σ^2_{F2} variance of F_2; σ^2_{BCP1} = variance of BCP_1; and σ^2_{BCP2} = variance of BCP_2.

Gain from selection and effective factors

Genetic gain from one cycle of selection was predicted by the SASQuant program using the method described by Hallauer and Miranda (1988):

$$\text{Gain} = h^2 \times \sqrt{\sigma^2_P} \times k$$

where:

h^2 = narrow sense heritability; σ^2_P = phenotypic variance; and k = constant for selection differential (for this study, 5%, 10% and 20% intensities were used).

To estimate the number of genes governing fiber traits in this study, effective factors estimations were calculated using the models by Wright (1968); Mather and Jinks (1982); and Lande (1981):

Wright's = $\frac{(\mu_{P1}-\mu_{P2})^2 \times \left\{1.5-[\,2 \times \frac{\mu_{F1}-\mu_{P1}}{\mu_{P1}-\mu_{P1}} \times \left(1-\frac{\mu_{F1}-\mu_{P1}}{\mu_{P2}-\mu_{P1}}\right)]\right\}}{8 \times [\,\sigma_{F2}^2 - \frac{\sigma_{P1}^2+\sigma_{P2}^2+(2\times\sigma_{F1}^2)}{4}]}$

Mather and Jinks' = $\frac{\frac{(\mu_{P1}-\mu_{P2})^2}{2}}{(2\times\sigma_{F2}^2)-(\sigma_{BCP1}^2+\sigma_{BCP2}^2)}$

Lande's model I = $\frac{(\mu_{P1}-\mu_{P2})^2}{8 \times [\,\sigma_{F2}^2 - \frac{\sigma_{P1}^2+\sigma_{P2}^2+(2\times\sigma_{F1}^2)}{4}]}$

Lande's model II = $\frac{(\mu_{P1}-\mu_{P2})^2}{8 \times [\,(2\times\sigma_{F2}^2)-(\sigma_{BCP1}^2+\sigma_{BCP2}^2)]}$

Lande's model III = $\frac{(\mu_{P1}-\mu_{P2})^2}{[8 \times (\sigma_{BCP1}^2+\sigma_{BCP2}^2-\sigma_{F1}^2)]-\frac{(\sigma_{P1}^2+\sigma_{P2}^2)}{2}}$

where:

$\sigma_{P1}^2, \sigma_{P2}^2, \sigma_{F1}^2, \sigma_{F2}^2, \sigma_{BCP1}^2$ and σ_{BCP2}^2 = variances for P_1, P_2, F_1, F_2, BCP_1 and BCP_2, respectively; μ_{P1}, μ_{P2} and μ_{F2} = means for P_1, P_2 and F_2, respectively.

With these models, the assumptions were made that genes segregating for traits of interests are all located in one parent, all genes are unlinked with equal effects, no G x E effects, and without epistatic or dominance effects (Tchiagam et al., 2011; Wright, 1968).

Results and discussions

Generations within each of the six families were different for fiber Elo-H, Str-H, UHML, UI and Mic with the exception of Str-H for the TAM x DEV family - an important requirement for effective generation means analysis (Table 15). Significant Gen x Year interaction was observed for five of the possible six families in the study for Elo-H with the exception of the TAM x DEV. Based on the magnitude of mean squares, generation differences explained a much larger portion of variation in Elo-H than the Gen x Year interaction, and year term was insignificant for all families. For Str-H, year was insignificant for all families and Gen x Year interaction was significant for all families. Generations explained a lesser degree of variation for fiber Str-H as some of the families exhibited larger degree of variations due to Gen x Year interaction and TAM x DEV family was insignificant for the Gen term. For fiber UHML, year was significant for the TAM x ARK, TAM x DEV, ARK x MD9, ARK x DEV and MD9 x DEV families. Gen x Year was significant for UHML in all families except for TAM x ARK and TAM x MD9 families. Similar to Elo-H, differences among generation constituted a larger portion of variations than the Gen x Year for UHML. Fiber UI varied across years for all families except for the MD9 x DEV family, whereas the Gen x Year for UI was significant for all families except for the TAM x DEV and ARK x MD9 families. For fiber Mic, TAM x DEV and ARK x DEV were two of the six possible families with significant year term and Gen x Year was significant for all families. For the six families used in this study, means for all traits were separated by year when significant Gen x Year interactions were reported (Table 15).

Table 15. Analysis of variance for HVI fiber properties for all GMA families in 2011 and 2012 in College Station, TX.

A. HVI Elo-H (%)

	Family‡					
S.O.V. †	TAM x ARK	TAM x MD9	TAM x DEV	ARK x MD9	ARK x DEV	MD9 x DEV
Year	28.78	12.01	28.29	26.33	47.59	22.86
Error A	19.38	5.74	9.68	12.34	15.14	25.06
Gen	42.60**	3.18**	28.78**	21.49**	10.59**	30.23**
Gen x Year	1.88**	1.27**	0.50	6.10**	3.37**	0.91*
Residual	0.22	0.30	0.34	0.40	0.55	0.38
CV (%)	6.67	8.02	7.53	8.28	8.86	7.84

B. HVI Str-H (kN m kg^{-1})

	Family‡					
S.O.V. †	TAM x ARK	TAM x MD9	TAM x DEV	ARK x MD9	ARK x DEV	MD9 x DEV
Year	164.65	32.79	124.60	70.21	3.27	153.98
Error A	51.55	50.96	98.91	36.31	54.23	39.60
Gen	94.75**	103.19**	8.41	164.75**	91.70**	16.24**
Gen x Year	22.29**	35.98**	23.84**	20.47**	67.11**	93.60**
Residual	3.24	6.02	5.53	4.94	5.45	6.52
CV (%)	5.28	7.11	6.58	6.57	6.79	7.26

C. HVI UHML (mm)

	Family‡					
S.O.V. †	TAM x ARK	TAM x MD9	TAM x DEV	ARK x MD9	ARK x DEV	MD9 x DEV
Year	2.38**	4.20	4.19**	1.77*	4.74**	3.88**
Error A	0.03	0.89	0.26	0.24	0.11	0.25
Gen	2.71**	0.32**	0.68**	1.37**	0.54**	0.57**
Gen x Year	0.03	0.04	0.22**	0.29**	0.28**	0.23**
Residual	0.05	0.02	0.02	0.02	0.03	0.03
CV (%)	3.15	3.55	3.6	3.91	4.54	4.35

*, ** Significant at 0.05 and 0.01 probability level, respectively; n/a, not available.
† Gen, Generation; Gen by Rep, Generation by replication; Gen x Year, Generation by year.
‡ TAM x ARK, TAM-B-182-33 x UA 48; TAM x MD9, TAM-B-182-33 x MD-9; TAM x DEV, TAM-B-182-33 x Dever; ARK x MD9, UA 48 x MD-9; ARK x DEV, UA 48 x Dever; MD9 x DEV, MD9 x Dever.

Table 15. Continued.

D. HVI UI (%)

	Family‡					
S.O.V. †	TAM x ARK	TAM x MD9	TAM x DEV	ARK x MD9	ARK x DEV	MD9 x DEV
Year	101.67**	100.72**	131.89*	38.43*	132.66**	97.67
Error A	4.45	4.8	18.89	3.35	9.45	16.57
Gen	29.75**	21.96**	12.36**	16.86**	10.03**	9.38**
Gen x Year	18.68**	19.91**	0.34	0.6	8.50**	12.29**
Residual	1.06	1.73	1.13	1.29	1.32	1.33
CV (%)	1.21	1.55	1.25	1.34	1.37	1.36

E. HVI Mic

	Family‡					
S.O.V. †	TAM x ARK	TAM x MD9	TAM x DEV	ARK x MD9	ARK x DEV	MD9 x DEV
Year	0.16	0.33	4.46*	4.94	17.26*	4.87
Error A	1.1	1.63	0.66	0.99	2.74	2.23
Gen	5.73**	6.17**	5.81**	3.09**	3.97**	0.33**
Gen x Year	7.32**	2.96**	2.80**	1.53**	2.07**	1.12**
Residual	0.14	0.17	0.16	0.14	0.15	0.18
CV (%)	8.93	10.75	10.55	9.23	9.48	11.40

*, ** Significant at 0.05 and 0.01 probability level, respectively; n/a, not available.
† Gen, Generation; Gen by Rep, Generation by replication; Gen x Year, Generation by year.
‡ TAM x ARK, TAM-B-182-33 x UA 48; TAM x MD9, TAM-B-182-33 x MD-9; TAM x DEV, TAM-B-182-33 x Dever; ARK x MD9, UA 48 x MD-9; ARK x DEV, UA 48 x Dever; MD9 x DEV, MD9 x Dever.

Based on means of the six generations within each family (Table 16), general trends observed across most families were: F_1 and F_2 means tend to be the mid-parent values of the two parents, and when the F_1s were crossed to the high parents, the backcross means were closer to the high parent means and similar observation applies when F_1s were crossed to the low parents. For fiber Elo-H, generations within families were significantly different except for the TAM x MD9 family in 2012 as a result of similar Elo-H values of the two parents. For fiber strength, all families reported strength values in the strong (294.2 kN m kg^{-1} – 313.8 kN m kg^{-1}) and very strong (>323.6 kN m kg^{-1}) range based on current U.S. cotton fiber property ratings (Cotton Incorporated, 2012). Due to the high Str-H nature of all parents selected for the study, further dissections on genetics of fiber Str-H behind these families would have minimal benefits. The same applies for fiber length as most of the families used in the study would be considered as long fibers (> 28.2 mm) based on current U.S. market ratings with the exception of ARK. For fiber UI, all families were highly uniform and although differences in uniformity were statistically significant among generations, there appears to be little biological significance in this narrow range of variation. Mic is a unique fiber property as it is a measurement that is confounded with maturity and fineness of cotton fibers. Improvement in fiber micronaire is usually not a concern as breeders would typically want to hold micronaire values constant and within a marketable range.

Table 16. Means of HVI fiber properties for six generations for GMA families in 2011 and 2012 in College Station, TX. †

A. HVI Elo-H (%)

	Family‡				
	TAM x ARK		TAM x MD9		TAM x DEV
Generation	2011	2012	2011	2012	2011/12
P_1	6.54 d	7.45 c	6.69 a	7.11 a	6.95 e
P_2	9.07 a	9.18 a	6.93 a	7.17 a	9.29 a
F_1	7.04 c	7.98 b	6.74 a	6.87 a	7.55 c
F_2	6.11 e	6.98 d	6.29 b	6.99 a	7.70 c
BCP_1	6.33 de	7.24 c	6.29 b	6.91 a	7.31 d
BCP_2	7.39 b	7.78 b	6.75 a	7.10 a	8.28 b

	Family‡					
	ARK x MD9		ARK x DEV		MD9 x DEV	
Generation	2011	2012	2011	2012	2011	2012
P_1	8.92 a	8.87 a	8.73 a	9.26 ab	6.94 d	7.28 d
P_2	6.82 c	7.48 e	8.93 a	9.70 a	9.07 a	9.47 a
F_1	7.93 b	7.98 cd	8.34 b	9.32 a	7.41 c	8.43 bc
F_2	6.83 c	8.24 bc	7.43 c	8.83 b	7.43 c	8.17 c
BCP_1	7.74 b	8.52 ab	8.11 b	8.79 b	7.00 d	7.49 d
BCP_2	6.83 c	7.80 de	7.96 b	8.82 b	8.02 b	8.64 b

† For each family, first parent listed is P_1 and second parent listed is P_2.
‡ TAM x ARK, TAM-B-182-33 x UA 48; TAM x MD9, TAM-B-182-33 x MD-9; TAM x DEV, TAM-B-182-33 x Dever; ARK x MD9, UA 48 x MD-9; ARK x DEV, UA 48 x Dever; MD9 x DEV, MD9 x Dever.
§ Mean values followed by the same letter are not different at $p < 0.05$ according to Waller LSD.
¶ Family with only one year of reported data.

Table 16. Continued.†

B. HVI Str-H (kN m kg^{-1})

	Family‡					
	TAM x ARK		TAM x MD9		TAM x DEV	
Generation	2011	2012	2011	2012	2011	2012
P_1	350.9 ab	326.4 ab	353.2 ab	343.0 a	357.1 a	337.2 a
P_2	309.1 d	289.5 c	338.3 bc	341.6 a	336.9 b	342.1 a
F_1	335.7 c	326.5 ab	338.6 bc	336.0 ab	369.3 a	343.6 a
F_2	339.3 bc	333.2 a	328.2 c	331.9 ab	362.2 a	339.1 a
BCP_1	356.7 a	330.1 ab	343.4 bc	328.4 b	354.7 ab	345.3 a
BCP_2	337.0 c	324.1 b	363.1 a	341.6 a	355.5 a	345.8 a

	Family‡					
	ARK x MD9		ARK x DEV		MD9 x DEV	
Generation	2011	2012	2011	2012	2011	2012
P_1	309.1 c	294.8 c	305.3 d	305.8 d	372.1 a	342.0 a
P_2	356.6 a	341.4 a	346.2 ab	349.0 a	361.1 ab	333.9 a
F_1	339.8 b	326.6 b	330.8 c	338.4 ab	357.8 ab	347.5 a
F_2	338.6 b	325.0 b	352.8 a	329.9 bc	349.6 b	337.6 a
BCP_1	318.4 c	322.9 b	335.3 bc	324.5 c	367.2 a	339.1 a
BCP_2	350.6 ab	340.8 a	337.1 bc	346.4 a	330.4 c	346.9 a

† For each family, first parent listed is P_1 and second parent listed is P_2.
‡ TAM x ARK, TAM-B-182-33 x UA 48; TAM x MD9, TAM-B-182-33 x MD-9; TAM x DEV, TAM-B-182-33 x Dever; ARK x MD9, UA 48 x MD-9; ARK x DEV, UA 48 x Dever; MD9 x DEV, MD9 x Dever.
§ Mean values followed by the same letter are not different at $p < 0.05$ according to Waller LSD.
¶ Family with only one year of reported data.

Table 16. Continued. †

C. HVI UHML (mm)

	Family‡			
	TAM x ARK	TAM x MD9	TAM x DEV	
Generation	2011/12	2011/12	2011	2012
P_1	31.5 b	31.8 ab	30.5 a	33.3 a
P_2	26.7 d	30.5 d	27.4 c	30.0 d
F_1	30.0 c	31.2 c	30.0 a	32.3 b
F_2	32.3 a	31.5 bc	30.5 a	31.5 c
BCP_1	31.8 b	32.0 a	30.5 a	32.0 b
BCP_2	30.0 c	31.8 ab	29.2 b	31.5 c

	Family‡					
	ARK x MD9		ARK x DEV		MD9 x DEV	
Generation	2011	2012	2011	2012	2011	2012
P_1	25.9 c	27.7 c	25.7 d	28.2 c	30.7 a	32.0 a
P_2	30.0 a	31.2 a	27.4 c	29.7 b	28.2 cd	29.2 c
F_1	28.4 b	29.5 b	27.7 bc	30.7 ab	29.7 b	31.2 ab
F_2	29.5 a	30.0 b	29.0 a	30.0 b	28.7 c	31.0 b
BCP_1	28.2 b	30.2 b	28.0 bc	29.7 b	29.7 b	31.8 ab
BCP_2	30.2 a	31.5 a	28.2 b	31.0 a	27.9 d	31.5 ab

† For each family, first parent listed is P_1 and second parent listed is P_2.
‡ TAM x ARK, TAM-B-182-33 x UA 48; TAM x MD9, TAM-B-182-33 x MD-9; TAM x DEV, TAM-B-182-33 x Dever; ARK x MD9, UA 48 x MD-9; ARK x DEV, UA 48 x Dever; MD9 x DEV, MD9 x Dever.
§ Mean values followed by the same letter are not different at $p < 0.05$ according to Waller LSD.
¶ Family with only one year of reported data.

Table 16. Continued. †

D. HVI UI (%)

	Family‡				
	TAM x ARK		TAM x MD9		TAM x DEV
Generation	2011	2012	2011	2012	2011/12
P_1	84.9 a	85.5 ab	84.7 a	85.6 ab	85.8 a
P_2	82.5 d	82.9 c	83.8 b	84.9 b	83.9 d
F_1	83.5 bc	85.3 b	83.9 b	86.1 a	85.3 b
F_2	83.4 c	86.0 a	83.2 b	85.3 ab	84.7 c
BCP_1	84.9 a	85.6 ab	84.6 a	85.0 b	85.0 bc
BCP_2	84.1 b	85.5 ab	84.8 a	85.6 ab	84.7 c

	Family‡				
	ARK x MD9	ARK x DEV		MD9 x DEV	
Generation	2011/12	2011	2012	2011	2012
P_1	83.1 c	82.4 c	83.5 d	84.5 a	85.4 ab
P_2	84.2 b	83.1 bc	84.8 bc	83.8 b	84.3 c
F_1	84.4 b	83.7 ab	85.5 a	84.5 a	85.8 a
F_2	84.5 ab	83.8 a	84.7 c	83.9 ab	85.1 b
BCP_1	84.4 b	83.8 ab	85.0 abc	84.5 a	85.4 ab
BCP_2	84.9 a	83.4 ab	85.4 ab	83.2 b	85.7 ab

† For each family, first parent listed is P_1 and second parent listed is P_2.
‡ TAM x ARK, TAM-B-182-33 x UA 48; TAM x MD9, TAM-B-182-33 x MD-9; TAM x DEV, TAM-B-182-33 x Dever; ARK x MD9, UA 48 x MD-9; ARK x DEV, UA 48 x Dever; MD9 x DEV, MD9 x Dever.
§ Mean values followed by the same letter are not different at $p < 0.05$ according to Waller LSD.
¶ Family with only one year of reported data.

Table 16. Continued. †

E. HVI Mic (units)

	Family‡					
	TAM x ARK		TAM x MD9		TAM x DEV	
Generation	2011	2012	2011	2012	2011	2012
P_1	4.50 b	4.25 ab	4.57 a	4.28 a	4.66 a	4.21 a
P_2	4.76 a	4.40 a	3.85 c	3.86 b	3.98 c	3.67 d
F_1	4.45 b	4.26 a	4.26 b	3.81 b	4.30 b	3.89 bc
F_2	3.41 c	4.25 ab	3.46 d	3.87 b	3.59 d	3.77 cd
BCP_1	4.38 b	4.05 b	4.20 b	4.01 ab	4.14 bc	4.01 ab
BCP_2	4.29 b	4.24 ab	3.79 c	3.82 b	4.06 c	3.59 d

	Family‡					
	ARK x MD9		ARK x DEV		MD9 x DEV	
Generation	2011	2012	2011	2012	2011	2012
P_1	4.88 a	4.30 a	4.95 a	4.41 a	3.64 b	3.79 ab
P_2	3.77 d	3.93 b	4.11 c	3.69 c	4.01 a	3.83 a
F_1	4.24 c	4.46 a	4.41 b	3.78 c	4.01 a	3.72 ab
F_2	4.26 c	3.94 b	4.07 c	3.88 bc	3.93 a	3.57 ab
BCP_1	4.61 b	3.92 b	4.56 b	4.02 b	3.94 a	3.62 ab
BCP_2	4.20 c	3.94 b	4.47 b	3.68 c	4.18 a	3.51 b

† For each family, first parent listed is P_1 and second parent listed is P_2.
‡ TAM x ARK, TAM-B-182-33 x UA 48; TAM x MD9, TAM-B-182-33 x MD-9; TAM x DEV, TAM-B-182-33 x Dever; ARK x MD9, UA 48 x MD-9; ARK x DEV, UA 48 x Dever; MD9 x DEV, MD9 x Dever.
§ Mean values followed by the same letter are not different at $p < 0.05$ according to Waller LSD.
¶ Family with only one year of reported data.

Prior to generation means analysis, fiber traits for all families were tested for homogeneity of variance in the F_2 generations (Table 17). Traits within families with significantly different F_2 variances were analyzed separately by year for better error control whereas traits with homogeneous variances were combined across years for ease of analysis (Gusmini et al., 2007). For TAM x ARK, 2011 data were omitted from the generation means analysis due to low numbers of F_2 individuals obtained for fiber analysis to prevent bias.

The ABCD scaling test determined the three parameter model without epistatic effects was satisfactory in explaining the majority (> 95%) of variations observed in all families for fiber Elo-H, thus, no estimation of epistatic effects was performed (Table 18). Additive gene effects were predominant in fiber Elo-H and no significant dominance effects were detected in any family in 2011 and 2012. Families with significant additive effects were: TAM x ARK in 2012, (0.54%); TAM x DEV in 2011/ 2012, (0.96%); ARK x MD9 in 2011 and 2012, (0.92% and 0.73%, respectively); and MD9 x DEV in 2011/2012, (1.06%). All reported additive gene effects were converted to absolute number due to sensitivity of Hayman's model to negative values as the positivity or negativity of additive effects is dependent on the direction of the parental combinations used. Hence, all values reported for additive gene effects would best be used solely to represent the magnitude of additive effects and no implication on the directions of the additive effects should be made.

Table 17. Test for homogeneity of variance on all HVI fiber traits for all GMA families in 2011 and 2012 in College Station, TX.

	Elo-H	Str-H	UHML	UI	Mic
Family†	(%)	(kN m kg^{-1})	(mm)	(%)	(units)
TAM x ARK¶	-	-	-	-	-
TAM x MD9	**	**	n/s	n/s	n/s
TAM x DEV	n/s	**	n/s	**	*
ARK x MD9	**	**	*	n/s	n/s
ARK x DEV	n/s	*	**	n/s	n/s
MD9 x DEV	n/s	**	**	n/s	n/s

*, ** Significant at 0.05 and 0.01 probability level, respectively. n/s, Non significant.
† TAM x ARK, TAM-B-182-33 x UA 48; TAM x MD9, TAM-B-182-33 x MD-9; TAM x DEV, TAM-B-182-33 x Dever; ARK x MD9, UA 48 x MD-9; ARK x DEV, UA 48 x Dever; MD9 x DEV, MD9 x Dever.
¶ Family with one year data included for analysis.

Similarly, the simple additive-dominance model was adequate in explaining the majority of variations observed in fiber Str-H (Table 18). Significant additive effects were observed in the ARK x MD9 family in 2011 and 2012 (32.2 and 17.9 kN m kg^{-1}, respectively), the ARK x DEV family in 2012 (21.9 kN m kg^{-1}) and the MD9 x DEV family in 2011 (37.2 kN m kg^{-1}). No dominance gene effects were detected for the parental materials used in this study. For fiber UHML, the scaling test indicated that additive x additive epistatic effect was significant in one family, i.e. TAM x ARK in 2012 (-4.3 mm). According to Mather and Jinks (1977), negative additive x additive estimates occurs when both parents are responsible for alleles contributing to the trait of interest and the gene pairs are in dispersive form. Under the three parameter model, no significant dominance effects in fiber UHML were detected for the parental combinations used in this study. The magnitude of significant additive effects for fiber UHML were, in descending order, ARK x MD9 in 2011 and 2012 (2.0 mm and 1.2 mm, respectively), MD9 x DEV in 2011 (1.8 mm), TAM x ARK in 2012 (1.6 mm), ARK x DEV in 2012 (1.1 mm) and TAM x DEV in 2011/12 (1.0 mm).

Non-allelic effects were not present in either fiber UI and Mic based on the scaling tests. Due to the overall similarities in fiber UI in parents used in the study, additive and dominance effects were largely negligible. For fiber Mic, significant additive values were reported by TAM x DEV with value of 0.42 units in 2012. The only significant dominance effects were reported by the TAM x DEV family in 2011 (2.0 units). However, the dominance effects diminished in 2012 suggesting a large environmental factor governing Mic in this family.

Table 18. Hayman's estimates for all HVI fiber traits in 2011 and 2012 in College Station, TX.

A. HVI Elo-H (%)

		Gene effects‡					
Family†	Year	*m*	*a*	*d*	*aa*	*ad*	*dd*
TAM x ARK§	2012	6.98**	0.54**	1.77	-	-	-
TAM x MD9	2011	6.23**	0.46	1.01	-	-	-
TAM x MD9	2012	6.99**	0.19	-0.22	-	-	-
TAM x DEV	2011/12	7.70**	0.96**	-0.19	-	-	-
ARK x MD9	2011	6.81**	0.92**	1.94	-	-	-
ARK x MD9	2012	8.24**	0.73*	-0.50	-	-	-
ARK x DEV	2011/12	8.15**	0.06	0.75	-	-	-
MD9 x DEV	2011/12	7.79**	1.06**	-0.23	-	-	-

B. HVI Str-H (kN m kg^{-1})

		Gene effects‡					
Family†	Year	*m*	*a*	*d*	*aa*	*ad*	*dd*
TAM x ARK§	2012	333.3**	5.9	-6.1	-	-	-
TAM x MD9	2011	329.6**	19.6	87.3	-	-	-
TAM x MD9	2012	331.9**	13.1	6.1	-	-	-
TAM x DEV	2011	362.1**	1.0	-4.9	-	-	-
TAM x DEV	2012	339.2**	0.6	30.0	-	-	-
ARK x MD9	2011	338.5**	32.2**	-8.8	-	-	-
ARK x MD9	2012	325.0**	17.9*	36.0	-	-	-
ARK x DEV	2011	353.0**	1.7	-62.1	-	-	-
ARK x DEV	2012	329.9**	21.9**	33.1	-	-	-
MD9 x DEV	2011	349.8**	37.2**	-12.8	-	-	-
MD9 x DEV	2012	337.5**	7.8	31.5	-	-	-

*, ** Significant at 0.05 and 0.01 probability level, respectively.

† TAM x ARK, TAM-B-182-33 x UA 48; TAM x MD9, TAM-B-182-33 x MD-9; TAM x DEV, TAM-B-182-33 x Dever; ARK x MD9, UA 48 x MD-9; ARK x DEV, UA 48 x Dever; MD9 x DEV, MD9 x Dever.

‡ *m*, mean; *a*, additive; *d*, dominance; *aa*, additive x additive; *ad*, additive x dominance; *dd*, dominance x dominance.

§ Family with one year data included for analysis.

Table 18. Continued.

C. HVI UHML (mm)

		Gene effects‡					
Family†	Year	*m*	*a*	*d*	*aa*	*ad*	*dd*
TAM x ARK§	2012	32.6**	1.6**	-3.3	-4.3**	-0.9	-0.8
TAM x MD9	2011/12	31.2**	0.3	2.7	-	-	-
TAM x DEV	2011/12	30.9**	1.0*	0.3	-	-	-
ARK x MD9	2011	29.6**	2.0**	-1.3	-	-	-
ARK x MD9	2012	29.9**	1.2*	3.5	-	-	-
ARK x DEV	2011	28.9**	0.3	-2.0	-	-	-
ARK x DEV	2012	29.9**	1.1*	3.5	-	-	-
MD9 x DEV	2011	28.8**	1.8**	0.3	-	-	-
MD9 x DEV	2012	31.2**	0.4	2.3	-	-	-

D. HVI UI (%)

		Gene effects‡					
Family†	Year	*m*	*a*	*d*	*aa*	*ad*	*dd*
TAM x ARK§	2012	86.0**	0.2	-0.6	-	-	-
TAM x MD9	2011/12	84.2**	0.4	3.4	-	-	-
TAM x DEV	2011	84.0**	0.4	0.8	-	-	-
TAM x DEV	2012	85.4**	0.3	1.1	-	-	-
ARK x MD9	2011/12	84.5**	0.6	1.5	-	-	-
ARK x DEV	2011/12	84.2**	0.0	1.6	-	-	-
MD9 x DEV	2011/12	84.5**	0.5	1.6	-	-	-

*, ** Significant at 0.05 and 0.01 probability level, respectively.

† TAM x ARK, TAM-B-182-33 x UA 48; TAM x MD9, TAM-B-182-33 x MD-9; TAM x DEV, TAM-B-182-33 x Dever; ARK x MD9, UA 48 x MD-9; ARK x DEV, UA 48 x Dever; MD9 x DEV, MD9 x Dever.

‡ *m*, mean; *a*, additive; *d*, dominance; *aa*, additive x additive; *ad*, additive x dominance; *dd*, dominance x dominance.

§ Family with one year data included for analysis.

Table 18. Continued.

E. HVI Mic (units)

		Gene effects‡					
Family†	Year	*m*	*a*	*d*	*aa*	*ad*	*dd*
TAM x ARK§	2012	4.25**	0.19	-0.46	-	-	-
TAM x MD9	2011/12	3.62**	0.30	1.22	-	-	-
TAM x DEV	2011	3.59**	0.10	2.00*	-	-	-
TAM x DEV	2012	3.77**	0.42*	0.06	-	-	-
ARK x MD9	2011/12	4.05**	0.25	0.51	-	-	-
ARK x DEV	2011/12	3.98**	0.21	0.62	-	-	-
MD9 x DEV	2011/12	3.75**	0.07	0.29	-	-	-

*, ** Significant at 0.05 and 0.01 probability level, respectively.
† TAM x ARK, TAM-B-182-33 x UA 48; TAM x MD9, TAM-B-182-33 x MD-9; TAM x DEV, TAM-B-182-33 x Dever; ARK x MD9, UA 48 x MD-9; ARK x DEV, UA 48 x Dever; MD9 x DEV, MD9 x Dever.
‡ *m*, mean; *a*, additive; *d*, dominance; *aa*, additive x additive; *ad*, additive x dominance; *dd*, dominance x dominance.
§ Family with one year data included for analysis.

For all families, variance components ($\sigma^2_{p,}$ σ^2_E, σ^2_A, and σ^2_D) were estimated to examine the contributions of various factors to the traits of interest and to determine the broad and narrow sense heritability (Table 19). Due to limitations on models used to estimate variance components, all negative variances were rounded to zero to enable heritability estimates. According to Wright's (1968) assumption, under ideal condition the F_2 variance should equal total phenotypic variance and should, in theory, be larger than the environmental variance which is derived from the variance components of non-segregating generation, i.e., P_1, P_2 and F_1. However, as observed in Table 19, such assumption may not always hold true. Based on empirical data by Gill and Jensen (1968), probability of obtaining negative estimates is directly influenced by the class

sizes and unbalanced dataset; in perspective of this study, those would be the number of individuals used for variance component estimates and the largely unbalanced degree of freedoms between the segregating and non-segregating generations.

For fiber Elo-H in all families, the additive component explained a larger portion of total genotypic variation than the dominance component, except for ARK x MD9 in 2011. Experimental error was a likely cause for the negative additive variance of ARK x MD9 as the backcross generations had larger variation than the F_2 generation. Overall, (excluding ARK x MD9 in 2011) narrow sense heritability for fiber Elo-H ranged from 0.29 to 0.62 and the highest narrow sense heritability in Elo-H was achieved by the TAM x MD9 in 2012.

For fiber Str-H, UHML, UI and Mic, the phenomenon of larger environmental variance than phenotypic or F_2 variance was observed for some of the families used in the study. The ARK x MD9 family consistently reported larger environmental variance in fiber Str-H, UHML and UI. Possible explanations may be that the non-segregating generations in this family was more sensitive to the growing environments in 2011 and 2012, and/or, the parents for this family were still segregating for some of the fiber traits measured. Recall that the parental plants were only reselected on Elo-S. In agreement with Hayman's estimates on additive versus dominance gene effects (Table 18), the additive variance components were much larger than the dominance variance components in most cases. This also means that the narrow sense heritability explained a significant portion of total heritability in fiber Str-H, UHML, UI and Mic in all families used in the study (Table 19).

Table 19. Variance components and narrow sense (h^2) heritability estimates for all HVI fiber traits in 2011 and 2012 in College Station, TX.

A. HVI Elo-H (%)

		Variance components‡§				Heritability
Family†	Year	σ^2_P	σ^2_E	σ^2_A	σ^2_D	h^2
TAM x ARK¶	2012	0.22	0.20	0.08	-0.05	0.29
TAM x MD9	2011	0.42	0.17	0.27	-0.02	0.61
TAM x MD9	2012	0.32	0.20	0.32	-0.19	0.62
TAM x DEV	2011/12	0.39	0.17	0.19	0.03	0.53
ARK x MD9	2011	0.28	0.18	-0.34	0.44	n/a
ARK x MD9	2012	0.50	0.36	0.19	-0.06	0.35
ARK x DEV	2011/12	0.63	0.56	0.42	-0.35	0.43
MD9 x DEV	2011/12	0.43	0.33	0.22	-0.12	0.40

† TAM x ARK, TAM-B-182-33 x UA 48; TAM x MD9, TAM-B-182-33 x MD-9; TAM x DEV, TAM-B-182-33 x Dever; ARK x MD9, UA 48 x MD-9; ARK x DEV, UA 48 x Dever; MD9 x DEV, MD9 x Dever.

‡ σ^2_P, phenotypic variance; σ^2_E, environmental variance; σ^2_A, additive variance; σ^2_D, dominance variance.

§ Negative variance components are assumed zero for heritability estimates.

¶ Family with one year data included for analysis.

n/a, not available due to negative σ^2_A.

Table 19. Continued.

B. HVI Str-H (kN m kg^{-1})

		Variance components‡§				Heritability
Family†	Year	σ^2_P	σ^2_E	σ^2_A	σ^2_D	h^2
TAM x ARK¶	2012	188.54	211.89	80.56	-103.90	0.28
TAM x MD9	2011	1235.40	760.22	1319.10	-843.90	0.63
TAM x MD9	2012	442.32	449.95	207.04	-214.70	0.32
TAM x DEV	2011	895.20	369.42	511.25	14.53	0.58
TAM x DEV	2012	343.20	275.31	112.48	-44.58	0.29
ARK x MD9	2011	619.23	674.30	135.01	-190.10	0.17
ARK x MD9	2012	359.28	250.56	21.79	86.92	0.08
ARK x DEV	2011	718.87	545.75	178.23	-5.10	0.25
ARK x DEV	2012	506.05	276.95	533.23	-304.10	0.66
MD9 x DEV	2011	956.33	1182.10	589.90	-815.70	0.33
MD9 x DEV	2012	481.18	426.37	164.09	-109.30	0.28

† TAM x ARK, TAM-B-182-33 x UA 48; TAM x MD9, TAM-B-182-33 x MD-9; TAM x DEV, TAM-B-182-33 x Dever; ARK x MD9, UA 48 x MD-9; ARK x DEV, UA 48 x Dever; MD9 x DEV, MD9 x Dever.

‡ σ^2_P, phenotypic variance; σ^2_E, environmental variance; σ^2_A, additive variance; σ^2_D, dominance variance.

§ Negative variance components are assumed zero for heritability estimates.

¶ Family with one year data included for analysis.

Table 19. Continued.

C. HVI UHML (mm)

		Variance components‡§				Heritability
Family†	Year	σ^2_P	σ^2_E	σ^2_A	σ^2_D	h^2
TAM x ARK¶	2012	1.30	0.86	1.30	-0.85	0.60
TAM x MD9	2011/12	1.55	1.44	0.98	-0.87	0.40
TAM x DEV	2011/12	1.42	0.79	0.71	-0.08	0.47
ARK x MD9	2011	1.12	0.84	-0.09	0.37	0.00
ARK x MD9	2012	1.37	1.62	-0.72	0.47	0.00
ARK x DEV	2011	1.29	1.50	0.55	-0.76	0.27
ARK x DEV	2012	2.96	1.94	3.37	-2.36	0.63
MD9 x DEV	2011	1.44	1.03	0.99	-0.58	0.49
MD9 x DEV	2012	2.47	1.57	1.47	-0.57	0.48

† TAM x ARK, TAM-B-182-33 x UA 48; TAM x MD9, TAM-B-182-33 x MD-9; TAM x DEV, TAM-B-182-33 x Dever; ARK x MD9, UA 48 x MD-9; ARK x DEV, UA 48 x Dever; MD9 x DEV, MD9 x Dever.

‡ σ^2_P, phenotypic variance; σ^2_E, environmental variance; σ^2_A, additive variance; σ^2_D, dominance variance.

§ Negative variance components are assumed zero for heritability estimates.

¶ Family with one year data included for analysis.

Table 19. Continued.

D. HVI UI (%)

		Variance components‡§				Heritability
Family†	Year	σ^2_P	σ^2_E	σ^2_A	σ^2_D	h^2
TAM x ARK¶	2012	0.97	1.93	0.27	-1.23	0.12
TAM x MD9	2011/12	2.34	1.38	2.14	-1.19	0.61
TAM x DEV	2011	1.22	0.92	-0.01	0.31	0.00
TAM x DEV	2012	1.23	0.70	0.60	-0.06	0.46
ARK x MD9	2011/12	1.19	1.68	-0.29	-0.20	0.00
ARK x DEV	2011/12	1.49	1.35	0.85	-0.72	0.39
MD9 x DEV	2011/12	1.51	0.91	0.68	-0.08	0.43

† TAM x ARK, TAM-B-182-33 x UA 48; TAM x MD9, TAM-B-182-33 x MD-9; TAM x DEV, TAM-B-182-33 x Dever; ARK x MD9, UA 48 x MD-9; ARK x DEV, UA 48 x Dever; MD9 x DEV, MD9 x Dever.

‡ σ^2_P, phenotypic variance; σ^2_E, environmental variance; σ^2_A, additive variance; σ^2_D, dominance variance.

§ Negative variance components are assumed zero for heritability estimates.

¶ Family with one year data included for analysis.

Table 19. Continued.

E. HVI Mic (units)

		Variance components‡§				Heritability
Family†	Year	σ^2_P	σ^2_E	σ^2_A	σ^2_D	h^2
TAM x ARK¶	2012	0.11	0.07	-0.04	0.07	0.00
TAM x MD9	2011/12	0.22	0.11	0.16	-0.05	0.59
TAM x DEV	2011	0.22	0.09	0.14	-0.02	0.61
TAM x DEV	2012	0.15	0.05	0.05	0.06	0.50
ARK x MD9	2011/12	0.14	0.11	0.03	0.00	0.21
ARK x DEV	2011/12	0.17	0.09	0.07	0.01	0.44
MD9 x DEV	2011/12	0.21	0.13	0.09	-0.01	0.41

† TAM x ARK, TAM-B-182-33 x UA 48; TAM x MD9, TAM-B-182-33 x MD-9; TAM x DEV, TAM-B-182-33 x Dever; ARK x MD9, UA 48 x MD-9; ARK x DEV, UA 48 x Dever; MD9 x DEV, MD9 x Dever.

‡ σ^2_P, phenotypic variance; σ^2_E, environmental variance; σ^2_A, additive variance; σ^2_D, dominance variance.

§ Negative variance components are assumed zero for heritability estimates.

¶ Family with one year data included for analysis.

The number of effective factors controlling fiber Elo-H ranged between 0.1 to 17.1 for Wright's method (1968), 0.0 to 19.5 for Mather and Jinks' method (1982) and 0.0 to 15.8, 0.0 to 4.9 and 0.0 to 3.3 for Lande's method I, II and III (1981), respectively (Table 20). All negative values for effective factors were omitted from discussions but were presented for the sake of unbiased comparisons. These negative values were due to the intrinsic limitations of the models used and could not be overcome by any statistical adjustments. The validity of effective factors depended heavily on the assumptions that genes are not linked, with equal effects, without G x E effects, no dominance and without epistatic interactions (Wright, 1968). For fiber Elo-H, no dominance or epistatic interactions were observed for all families in the study (Table 19). Overall, across all models, highest numbers of effective factors was obtained via Mather and Jinks method (1982). Using this model, TAM x ARK, TAM x DEV and MD9 x DEV were the three families with the highest number of effective factors for Elo-H. This would be an indication that the parents in these combinations were carrying different sets of genes or loci for Elo-H. To the contrary, zero or close to zero effective factors were estimated for the TAM x MD9 in 2011 and 2012 and ARK x DEV in 2011/12, which means that both parents were carrying identical sets of genes or loci responsible for fiber Elo-H. Average estimated gain from selection in Elo-H with 5%, 10% and 20% selection intensities were 0.6%, 0.5% and 0.4%, respectively, for all families. Highest gain of 0.8% Elo-H was achieved by the TAM x MD9 family in 2011 with 5% selection intensity. No predicted gain in Elo-H was estimated for ARK x MD9 in 2011 due to negative additive variance obtained for their narrow sense heritability estimate (Table 19).

The numbers of effective factors estimated for fiber strength were close to zero for most of the families suggesting that most parents used in the study were carrying similar Str-H genes (Table 20). This observation resonates to previous comments that most parental materials used for this study were high in Str-H because of breeders concern for the importance of strength under current U.S. cotton classing standards (Table 16). In 2012, the ARK x MD9 family reported unusually high numbers of effective factors, especially with the Mather and Jinks (1982) method. However, these values were of little value due to larger observed variations in the backcross generations than the F_2 generation for this family (data not shown). Average gain in Str-H under 5%, 10% and 20% selection intensities were 18.6 kN m kg^{-1}, 15.9 kN m $kg^{-1}$and 12.6 kN m kg^{-1}, respectively. Similar to results of fiber Str-H, effective factors estimated for fiber UHML and UI were low in most families in 2011 and 2012 with the exception of TAM x ARK in 2012 with Mather's model. The high UI nature of parental materials used for this study would mean that further extrapolation of the results would yield little biological meanings. Average UHML gains for all families under 5%, 10% and 20% intensities were 1.3 mm, 1.1 mm and 0.9 mm, respectively. Whereas for fiber UI, average gains were 1.1%, 0.9% and 0.7%, respectively. As previously discussed, most cotton breeding efforts would prefer to maintain Mic values within a marketable range; thus, the estimated effective factors and gain from selection would yield little practical benefits.

Table 20. Effective gene estimates and gain from selection for all HVI fiber traits in 2011 and 2012 in College Station, TX.

A. HVI Elo-H (%)

		Effective gene estimates					Genetic gain		
Family†	Year	Wright's	Mather's	Lande I	Lande II	Lande III	5%	10%	20%
TAM x ARK§	2012	17.1	19.5	15.8	4.9	-12.6	0.3	0.2	0.2
TAM x MD9	2011	0.1	0.1	0.0	0.0	0.0	0.8	0.7	0.6
TAM x MD9	2012	0.1	0.0	0.0	0.0	0.0	0.7	0.6	0.5
TAM x DEV	2011/12	3.4	14.5	3.1	3.6	2.7	0.7	0.6	0.5
ARK x MD9	2011	5.3	-6.6	5.3	-1.7	1.0	n/a‡	n/a	n/a
ARK x MD9	2012	1.9	5.0	1.8	1.2	3.3	0.5	0.4	0.3
ARK x DEV	2011/12	0.6	0.1	0.2	0.0	0.0	0.7	0.6	0.5
MD9 x DEV	2011/12	6.3	10.6	6.1	2.6	-20.2	0.5	0.5	0.4
						Average:	0.6	0.5	0.4

† TAM x ARK, TAM-B-182-33 x UA 48; TAM x MD9, TAM-B-182-33 x MD-9; TAM x DEV, TAM-B-182-33 x Dever; ARK x MD9, UA 48 x MD-9; ARK x DEV, UA 48 x Dever; MD9 x DEV, MD9 x Dever.

‡ n/a, value omitted due to negative additive estimate.

§ Family with one year data included for analysis.

Table 20. Continued.

B. HVI Str-H (kN m kg^{-1})

		Effective gene estimates					Genetic gain		
Family†	Year	Wright's	Mather's	Lande I	Lande II	Lande III	5%	10%	20%
TAM x ARK§	2012	-11.0	8.5	-7.3	2.1	-1.3	7.9	6.8	5.4
TAM x MD9	2011	0.1	0.1	0.1	0.0	-0.1	45.6	39.0	31.0
TAM x MD9	2012	-1.4	0.0	0.0	0.0	0.0	13.9	11.8	9.4
TAM x DEV	2011	0.3	0.4	0.1	0.1	0.1	35.7	30.5	24.3
TAM x DEV	2012	0.1	0.1	0.0	0.0	0.1	11.1	9.5	7.5
ARK x MD9	2011	-5.3	8.3	-5.1	2.1	-1.1	8.7	7.4	5.9
ARK x MD9	2012	2.7	49.8	2.5	12.4	1.4	3.1	2.7	2.1
ARK x DEV	2011	1.2	4.7	1.2	1.2	1.2	13.8	11.8	9.4
ARK x DEV	2012	1.2	1.8	1.0	0.4	-3.1	30.6	26.1	20.8
MD9 x DEV	2011	-0.2	0.1	-0.1	0.0	0.0	21.0	18.0	14.3
MD9 x DEV	2012	0.6	0.2	0.1	0.0	-0.1	12.7	10.8	8.6
						Average:	18.6	15.9	12.6

† TAM x ARK, TAM-B-182-33 x UA 48; TAM x MD9, TAM-B-182-33 x MD-9; TAM x DEV, TAM-B-182-33 x Dever; ARK x MD9, UA 48 x MD-9; ARK x DEV, UA 48 x Dever; MD9 x DEV, MD9 x Dever.
§ Family with one year data included for analysis.

Table 20. Continued.

C. HVI UHML (mm)

		Effective gene estimates					Genetic gain		
Family†	Year	Wright's	Mather's	Lande I	Lande II	Lande III	5%	10%	20%
TAM x ARK§	2012	7.7	9.7	7.1	2.4	-7.6	1.4	1.2	1.0
TAM x MD9	2011/12	1.5	0.7	1.5	0.2	-0.2	1.0	0.9	0.7
TAM x DEV	2011/12	2.4	7.5	2.1	1.9	2.4	1.2	1.0	0.8
ARK x MD9	2011	7.6	-92.1	7.5	-23.0	3.2	n/a‡	n/a	n/a
ARK x MD9	2012	-5.7	-7.8	-5.7	-2.0	6.3	n/a	n/a	n/a
ARK x DEV	2011	-3.5	3.2	-2.1	0.8	-0.5	0.6	0.5	0.4
ARK x DEV	2012	1.0	0.4	0.3	0.1	-0.3	2.2	1.9	1.5
MD9 x DEV	2011	1.7	2.9	1.7	0.7	-4.5	1.2	1.0	0.8
MD9 x DEV	2012	1.2	2.6	1.1	0.7	2.9	1.6	1.3	1.1
						Average:	1.3	1.1	0.9

† TAM x ARK, TAM-B-182-33 x UA 48; TAM x MD9, TAM-B-182-33 x MD-9; TAM x DEV, TAM-B-182-33 x Dever; ARK x MD9, UA 48 x MD-9; ARK x DEV, UA 48 x Dever; MD9 x DEV, MD9 x Dever.

‡ n/a, value omitted due to negative additive estimate.

§ Family with one year data included for analysis.

Table 20. Continued.

D. HVI UI (%)

		Effective gene estimates					Genetic gain		
Family†	Year	Wright's	Mather's	Lande I	Lande II	Lande III	5%	10%	20%
TAM x ARK§	2012	-1.2	12.2	-0.9	3.0	-0.4	0.2	0.2	0.2
TAM x MD9	2011/12	0.1	0.2	0.1	0.0	-0.4	1.9	1.6	1.3
TAM x DEV	2011	2.2	-177.0	2.0	-44.2	1.0	n/a‡	n/a	n/a
TAM x DEV	2012	0.7	2.1	0.6	0.5	0.7	1.1	0.9	0.7
ARK x MD9	2011/12	-0.7	-2.3	-0.3	-0.6	-0.2	n/a	n/a	n/a
ARK x DEV	2011/12	3.4	0.6	1.0	0.2	-0.2	1.0	0.8	0.7
MD9 x DEV	2011/12	0.4	0.6	0.2	0.2	0.2	1.1	0.9	0.7
						Average:	1.1	0.9	0.7

† TAM x ARK, TAM-B-182-33 x UA 48; TAM x MD9, TAM-B-182-33 x MD-9; TAM x DEV, TAM-B-182-33 x Dever; ARK x MD9, UA 48 x MD-9; ARK x DEV, UA 48 x Dever; MD9 x DEV, MD9 x Dever.

‡ n/a, value omitted due to negative additive estimate.

§ Family with one year data included for analysis.

Table 20. Continued.

E. HVI Mic (units)

		Effective gene estimates					Genetic gain		
Family†	Year	Wright's	Mather's	Lande I	Lande II	Lande III	5%	10%	20%
TAM x ARK§	2012	0.1	-0.3	0.1	-0.1	0.0	n/a‡	n/a	n/a
TAM x MD9	2011/12	0.4	1.0	0.4	0.2	0.7	0.6	0.5	0.4
TAM x DEV	2011	0.5	1.6	0.5	0.4	0.5	0.6	0.5	0.4
TAM x DEV	2012	0.4	3.3	0.4	0.8	0.2	0.4	0.3	0.3
ARK x MD9	2011/12	2.2	9.3	2.1	2.3	1.9	0.2	0.1	0.1
ARK x DEV	2011/12	1.1	4.3	1.0	1.1	0.9	0.4	0.3	0.3
MD9 x DEV	2011/12	0.1	0.2	0.1	0.1	0.1	0.4	0.3	0.3
						Average:	0.4	0.3	0.3

† TAM x ARK, TAM-B-182-33 x UA 48; TAM x MD9, TAM-B-182-33 x MD-9; TAM x DEV, TAM-B-182-33 x Dever; ARK x MD9, UA 48 x MD-9; ARK x DEV, UA 48 x Dever; MD9 x DEV, MD9 x Dever.

‡ n/a, value omitted due to negative additive estimate.

§ Family with one year data included for analysis.

CHAPTER VI

SUMMARY OF GENERATION MEANS ANALYSIS

All six generations within each family exhibited variability in Elo-H values with the exception of the TAM x MD9 family due to similar Elo-H values for both parents used for the family (Table 15). Experimental line DEV, with parental Elo-S of 7.6%, when used as a parent, consistently exhibited high Elo-H ranging from 9.29% in the TAM x DEV family in 2011/12 to 9.70% in the ARK x DEV family in 2012. The efficacy of the DEV experimental line as a potential donor for fiber Elo-H was shown further by the high F_2 means when crossed with diverse genotypes of upland cotton genotypes used in this study. When comparing Elo-H means across years by family (when applicable), generation means were, in general, higher in 2012 than in 2011. Such upward trend was observed in fiber UHML and to a lesser degree, in fiber and UI suggesting that 2012 was a more conducive year for cotton quality (Table 16).

As determined by the ABCD scaling test, no significant epistatic interaction was observed in all families as the three parameter model explained more than 95% of total variations observed in fiber Elo-H, Str-H, UI and Mic (Table 18). Significant non- allelic interactions were observed in UHML for TAM x ARK in 2012. Additive gene effects were the only significant gene effects detected for fiber Elo-H in this study, which corresponded well with multiple previous studies by May and Green, (1994), Miller and Rawling, (1967), and Quisenberry, (1975). Elo-H additive variance explained a much larger portion of the total genotypic variation than did dominance variance (Table 19).

High numbers of effective factors for Elo-H were identified for the TAM x ARK family in 2012 and the TAM x DEV family in 2011/12 with Mather's model. Since the parent TAM was present in both families, and low levels of effective factors were identified in the ARK x DEV family, it is tempting to conclude that TAM had a distinctive gene pool for Elo-H but not different than that of MD9 due to the low to zero effective factors between the TAM and MD9. In the same context, ARK and DEV may be carrying similar genes but on opposite ends as the high parental Elo-H of DEV was nullified by ARK (Table 20).

In conclusion, there was more variation in fiber Elo-H than fiber Str-H, UHML, UI or Mic in all families used in this study as indicated by the means (Table 16) and effective factor estimates (Table 20). All parental materials in this study were elite materials representing major cotton breeding programs in the U.S., and should therefore, have minimal variations within genotypes for Str-H, UHML, UI and Mic. However, due to the absence of standardized Elo-H measurements and the lack of emphasis on Elo-H during the development of these parental genotypes, Elo-H may vary considerably among these breeding programs. This means that selection in Elo-H within these families that are stable for all other important fiber traits could still result in significant gain.

CHAPTER VII

CONCLUSIONS

Diallel study for fiber elongation with five representative parental genotypes has demonstrated that additive gene action in fiber elongation far outweighs the dominance gene effects. Comparing the mean squares of GCA and SCA for fiber elongation, GCA explained many folds more of the total variations observed in the study. This would suggest that fiber elongation is a trait that can be easily selected for and improved using traditional pedigree breeding scheme. The study has determined two of the seven parental genotypes used, i.e. PSC and DEV to be superior combiners for fiber elongation. These two parents may serve as good sources of fiber elongation for future breeding efforts as they also represent two very significant breeding environments in the U.S. When elongation was measured using the Stelometer, elongation values were consistently lower than that of HVI. Both HVI and Stelometer reported very low C.V.s in elongation, suggesting that despite all the differences in instrumentations and testing protocols, the two instruments are very precise. Such observation was further testified by the high correlation between Elo-H and Elo-S in 2010 and 2011.

Data reported by generation means analysis herein supports conclusions by May and Green, (1994), Miller and Rawlings, (1967) and Quisenberry, (1975) that fiber elongation is primarily governed by additive gene action and to a lesser degree by dominance gene action. Epistatic gene effects were insignificant for fiber elongation as indicated by the ABCD scaling test. Based on the number of effective factors identified in this study, there are two distinctive gene pools for fiber elongation, one represented by TAM and MD9 and the other by ARK and DEV. For breeders interested in breeding for high elongation upland cotton, crossing between these two gene pools may help to diversify genetics in fiber elongation. For all families, larger variation was observed for fiber elongation as compared to the other fiber traits included in this study. With the representative parental genotypes used, this may be a good indication that fiber elongation is still segregating in these otherwise stable genotypes. This would also mean that reselection in current U.S. upland cultivars could result in significant gain in elongation.

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